SPATIAL AND TEMPORAL VARIABILITY OF SOIL CO$_2$ AND N$_2$O FLUXES IN TROPICAL FOREST SOILS: THE INFLUENCE OF TREE SPECIES, PRECIPITATION, AND SOIL TEXTURE

by

Joost Lambertus Maria van Haren

A Dissertation Submitted to the Faculty of the
DEPARTMENT OF SOIL, WATER, AND ENVIRONMENTAL SCIENCE
In Partial Fulfillment of the Requirement
For the degree of

DOCTOR OF PHILOSOPHY

In the Graduate College

THE UNIVERSITY OF ARIZONA

2011
As members of the Dissertation Committee, we certify that we have read the dissertation prepared by Joost van Haren entitled: Spatial and Temporal Variability of Soil CO$_2$ and N$_2$O Fluxes in Tropical Forest Soils: the Influence of Tree Species, Precipitation, and Soil Texture and recommend that it be accepted as fulfilling the dissertation requirement for the Degree of Doctor of Philosophy.

Date: 04/15/11
Dr. Scott Saleska

Date: 04/15/11
Dr. Jon Chorover

Date: 04/15/11
Dr. Martha Hawes

Date:

Final approval and acceptance of this dissertation is contingent upon the candidate’s submission of the final copies of the dissertation to the Graduate College.

I hereby certify that I have read this dissertation prepared under my direction and recommend that it be accepted as fulfilling the dissertation requirement.

Date: 04/22/11
Dissertation Director: Dr. Scott Saleska
STATEMENT BY AUTHOR

This dissertation has been submitted in partial fulfillment of requirements for an advanced degree at the University of Arizona and is deposited in the University Library to be made available under rules of the Library.

Brief quotations from this dissertation are allowable without special permission, provided that accurate acknowledgment of source is made. Requests for permission for extended quotation from or reproduction of this manuscript in whole or in part may be granted by the head of the major department or the Dean of the College of Agriculture and Life Sciences when in his or her judgment the proposed use of the material is in the interest of scholarship. In all other instances, however, permission must be obtained from the author.

SIGNED: Joost van Haren
ACKNOWLEDGEMENTS

This work could not have been completed without the help and support from numerous people who have helped me and my family throughout the process. Before I name people, I would like to acknowledge all those who have helped me.

On the scientific side, I would like to thank Dr. Scott Saleska for his unwavering support and his knack for always finding the issues I had forgotten during our discussions. I also thank Scott for opening the door to Brazil for me. I thank Dr. Jon Chorover and Martha Hawes for many thought provoking discussions and being here at the end. The Saleska lab people, who always provided a listening ear and curious mind, and were fabulous to work together with to solve problems. In particular I would like to thank Brad Christoffersen and Scott Stark for their help with R issues, Natalia Restrepo for her help with Arc-GIS analysis and general data retrieval for the Amazon basin, Virginia Rich for always being so supportive and reading through my early drafts. I also would like to thank Brian McGill for the many good suggestions on data analysis. Last, but certainly not least, I would like to thank all the people that helped, many of them became very good friends, during my field work in Brazil. Special thanks go to my friends Cleuton Perreira and Raimundo Cosme de Oliveira Jr., without their support, help and friendship this thesis would never have been completed.

On the more personal side, I would like to thank all our friends in Tucson for their support and of course I need to thank my family who always supported and believed in me. They were always confident I would complete this process.

Lastly, I would like to posthumously thank Dr. Dean Martens for encouraging me to endeavor along the PhD path. To my regret Dean was not able to see me through most of the process. I miss his frank approach to science.
DEDICATION

To my darling wife and daughters

Allison,

Fiona,

and

Nadine

To my mother

Anneke van Haren-Houx
# TABLE OF CONTENTS

LIST OF FIGURES .................................................................................................................. 10

LIST OF TABLES ....................................................................................................................... 15

ABSTRACT ................................................................................................................................. 16

INTRODUCTION ......................................................................................................................... 19
  1.1 Context of Research ......................................................................................................... 19
  1.2 Statement of the objectives ............................................................................................ 22

PRESENT STUDY ....................................................................................................................... 24
  2.1 Summary of paper 1: Spatial and temporal variability of soil CO₂ and N₂O fluxes in a clay-rich site in the Tapajos National Forest, east-central Amazonia, Brazil. .... 26
  2.2 Summary of paper 2: Do plant species influence soil CO₂ and N₂O fluxes in a diverse tropical forest .............................................................................................................. 31
  2.3 Summary of paper 3: Tropical tree species effects on soil properties and greenhouse gas fluxes in monoculture and diverse forests ............................................................................ 35
  2.4 Summary of paper 4: Forest growth rate predicts tropical soil N₂O fluxes. ........ 39
  2.5 Summary and Conclusions of this Doctoral Research Program .................................. 44

REFERENCES ............................................................................................................................. 47

APPENDIX A SPATIAL AND TEMPORAL VARIABILITY OF SOIL CO₂ AND N₂O FLUXES IN A CLAY-RICH SITE IN THE TAPAJOS NATIONAL FOREST, EAST-CENTRAL AMAZONIA, BRAZIL ................................................................................................................................. 54
# TABLE OF CONTENTS - Continued

Abstract ................................................................................................................................. 56  
Introduction .......................................................................................................................... 58  
Methods ............................................................................................................................... 61  
Results ................................................................................................................................. 65  
Discussion ........................................................................................................................... 67  
Conclusion ......................................................................................................................... 73  
References ......................................................................................................................... 75  
Figure captions .................................................................................................................. 84

APPENDIX B DO PLANT SPECIES INFLUENCE SOIL CO₂ AND N₂O FLUXES IN A DIVERSE TROPICAL FOREST? .......................................................... 94

Abstract ................................................................................................................................. 95  
1 Introduction ........................................................................................................................ 95  
2 Methods ............................................................................................................................ 96  
  2.1 Site description ........................................................................................................... 96  
  2.2 Sampling design and analysis .................................................................................... 96  
  2.3 Soil gas fluxes ............................................................................................................ 97  
  2.4 Data analyses ........................................................................................................... 97  
  2.5 Impact of species composition on ecosystem-scale fluxes ....................................... 97  
3 Results ............................................................................................................................... 97  
  3.1 Overall flux and soil parameter differences ............................................................... 97  
  3.2 Flux and soil parameter differences with species grouped by day ......................... 97  
  3.3 Species-specific regressions ..................................................................................... 100  
  3.4 Soil measurements near species with differing N₂O fluxes ..................................... 100  
  3.5 Impact of tree species on ecosystem fluxes ............................................................... 100  
4 Discussion ......................................................................................................................... 101  
  4.1 Potential causes for CO₂ flux differences ................................................................. 101  
  4.2 Potential causes for N₂O flux differences ................................................................. 101  
    4.2.1 N₂O fluxes and legume species ....................................................................... 101  
    4.2.2 Potential plant drivers of soil biogeochemistry ............................................... 101  
5 Conclusions ....................................................................................................................... 102  
References ............................................................................................................................ 102
TABLE OF CONTENTS - Continued

APPENDIX C TROPICAL TREE SPECIES EFFECTS ON SOIL PROPERTIES AND GREENHOUSE GAS FLUXES IN MONOCULTURE AND DIVERSE FORESTS ............................................. 104

Abstract........................................................................................................................................106
1 Introduction ....................................................................................................................................108
2 Methods and site description ......................................................................................................110
   2.1 Site description and species selection ..................................................................................110
   2.2 Flux and supporting measurements ....................................................................................112
   2.3 Statistical analyses ..............................................................................................................114
3 Results .........................................................................................................................................115
   3.1 Plantation vs forest overall ..................................................................................................115
   3.2 Tree species differences ......................................................................................................115
   3.3 Regression analysis and structural equation modeling .......................................................117
4 Discussion .....................................................................................................................................119
   4.1 Overall comparison forest vs. plantation .............................................................................119
   4.2 Species differences in monoculture ....................................................................................121
   4.3 Predictive capability of plantation for tree growth and soil properties in forest settings ...124
   4.4 Effects of climate and vegetation drivers on soil processes on the plantation vs. forest ...125
5 Conclusions ...................................................................................................................................127
Acknowledgements ......................................................................................................................128
References ......................................................................................................................................129
Tables .............................................................................................................................................141
Figure captions ............................................................................................................................146

APPENDIX D FOREST GROWTH PREDICTS TROPICAL SOIL N₂O FLUXES .................... 153

Abstract .........................................................................................................................................155
Introduction .....................................................................................................................................156
Concept ..........................................................................................................................................157
Methods .........................................................................................................................................160
Results ...........................................................................................................................................162
Discussion and conclusions .........................................................................................................163
TABLE OF CONTENTS - Continued

References .............................................................................................................................................. 168
Tables .................................................................................................................................................. 175
Figure captions .................................................................................................................................. 176
Supplemental methods and figures .................................................................................................... 182
  Process based models ...................................................................................................................... 183
  References ...................................................................................................................................... 184
  Figure captions .............................................................................................................................. 185
LIST OF FIGURES

A.1 Our sampling scheme at the km 67 eddy covariance site in the Tapajos National Forest, ~67 km south of Santarem, Para, Brazil. Forest inventory transects were located to capture forest dynamics in the area most influential to the eddy flux tower. Dots along the transects denote the spatial soil sampling locations. The temporal sampling locations are located close to the tower as indicated by the arrows.................................................................87

A.2 Soil CO$_2$ (top) and N$_2$O (Bottom) flux distributions from the three chamber datasets. The temporal datasets (automated and manual were separated in dry (July through Oct) and wet season (February through May) part of the dataset, the transition months were not shown .................................................................88

A.3 Seasonality of soil gas fluxes coincides with precipitation variability. Bottom graph contains the temporal variability of precipitation (grey bars) and measured (black dots) and modeled (red line) soil water content. The center graph contains N$_2$O fluxes from automated (blue line) and manual (black dots) chambers and modeling results (red line). The top graph CO$_2$ fluxes for the automated (blue line) and manual (black dots) chambers. For clarity the points have been connected by a line, which does not reflect a filling method .................................................................................................................................89

A.4 Large spatial soil gas flux variability is apparent from individual automated chamber soil CO$_2$ (top) and N$_2$O (bottom) flux trends with time. Each color denotes a different chamber. The colors in the two graphs do not necessarily correspond to the same chamber .................................................................................................................................90

A.5 Regression plots of the monthly soil CO$_2$ (top) and N$_2$O (bottom) fluxes and (from left to right) tree growth rate, soil temperature, precipitation, and soil moisture (%WFPS). The trend lines all (except for CO$_2$ and soil temperature) were highly significant at P < 0.0001. CO$_2$ fluxes are bi-modally related to soil temperature, we therefore separated the data in dry (closed diamonds, July though October), transition (open squares, November through January and June) and wet season (closed triangles, February through May) .................................................................................................................................91
A.6 Structural equation modeling of monthly climate forest dynamics, and soil \( \text{N}_2\text{O} \) fluxes suggests that precipitation and tree growth are the strongest predictors for soil \( \text{N}_2\text{O} \) fluxes. Precipitation both directly and through air temperature are the most important driver for the daily \( \text{CO}_2 \) variation. Arrow size and superscripts indicate the P-value of each regression or path. Also given for each path are the unstandardized coefficient –or slope- and standard error.

A.7 Structural equation modeling of monthly climate forest dynamics, and soil \( \text{N}_2\text{O} \) fluxes. Precipitation both directly and through air temperature are the most important driver for the daily \( \text{CO}_2 \) variation. The significance of soil moisture on monthly \( \text{N}_2\text{O} \) flux becomes only marginally significant (\( P=0.06 \)) when the path between soil temperature and \( \text{N}_2\text{O} \) flux is removed (not shown). Arrow size and superscripts indicate the P-value of each regression or path. Also given for each path are the unstandardized coefficient –or slope- and standard error.

B.1 (a) Tree mass growth rate (MGR), (b) soil pH, (c) bulk density (BD), (d) \%WFPS, (e) \( \text{CO}_2 \) flux, and (f) \( \text{N}_2\text{O} \) flux in relation to tree species at three clay-rich sites in the TNP. All values were corrected for mean differences between sampling days. Horizontal continuous and dashed lines denote overall mean (\( n = 338 \)) and 95% confidence interval (CI), respectively, while black diamonds and error bars denote species means \( \pm 95\% \) CI. Legume (L) species are denoted with shading, and species means significantly greater and smaller at \( \alpha = 0.01 \) are denoted with + or -, respectively. AL, Astronium lecointei (\( n = 17 \)); BE, Bertholletia excelsa (\( n = 11 \)); CG, Carapa guianensis (\( n = 28 \)); CM, Coipefeira multijuga (\( n = 7 \)); CS, Couratari stellata (\( n = 32 \)); CV, Caryocar villosum (\( n = 23 \)); CX, Chameacrista xinguensis (\( n = 13 \)); EU, Erisma uncinatum (\( n = 29 \)); LL, Lecythis lurida (\( n = 33 \)); MH, Manilkara huberi (\( n = 35 \)); PP, Psuedopitadenia psilostachya (\( n = 22 \)); PR, Pouteria reticulate (\( n = 18 \)); SC, Sclerolobium chrysophyllum (\( n = 16 \)); SM, Schefflera morototoni (\( n = 7 \)), and VM, Vochysia maxima (\( n = 17 \)). Asterisk denotes control taken > 10 m from any tree > 35 cm (\( n = 33 \)).

B.2 Soil \( \text{CO}_2 \) fluxes versus (a) \( T_{\text{soil}} \), (b) BD, (c) liana DBH, and (d) their multiple regression combination. The multiple regression explains \(~23\%\) of \( \text{CO}_2 \) flux variability. BD includes information on soil moisture (\%WFPS) and total organic content (TOC in top 0-3 cm of...
the soil), since BD explains ~55% and 45% of variability in %WFPS and TOC, respectively.

B. 3 Species-specific soil N\textsubscript{2}O fluxes versus (a) %WFPS, (b) mass growth rate (MGR), and (c) their combination. Vochysiaceae N\textsubscript{2}O fluxes ($r^2_{\text{adj}} = 0.97$ (large dashed line) versus 0.39 (solid line) for all species) define a separate, more positive trend with %WFPS than most other species (small dashed line, $r^2_{\text{adj}} = 0.70$). The negative trend between N\textsubscript{2}O flux and MGR is significant, especially when S. morototoni, a pioneer species, is excluded ($r^2_{\text{adj}} = 0.48$ and 0.69, respectively). Note that because of the negative correlation with N\textsubscript{2}O, the sign of the MGR and %WFPS coefficients is the opposite of what is expected.

C.1 Map of Brazil with site locations and detailed transect information for the established forest sites in the Tapajos National Forest (TNF) bound by the BR-163 on the east and Tapajos river on the west. The plantation is highlighted on the top left, with the letters denoting the different species plots (AL = A. lecontei, BE = B. excelsa, CG = C. guinanensis, CM = C. Multijuga (legume), CV = C. villosum, HE = H. Excelsum (legume), LL = L. Lurida, MH = M. Huberi, SC = S. Chrysophyllum (legume), and VM = V. Maxima).

C.2 Box plots by species of all measured variables both in the forest (grey filled boxes) and plantation (open boxes). ANOVA results are represented by both the $R^2$ (variance explained) and P-value. Stars above or below the box and whiskers indicate variables that differ between forest and plantation (*=0.05, **=0.01, ***=0.001, and ****=0.0001). The capital letter next to the boxes indicate species differences ($\alpha=0.01$); lower case letters indicate species differences within the plantation.

C.3 Semi-variogram plots of bulk density (BD), soil moisture (WFPS), CO\textsubscript{2} and N\textsubscript{2}O flux for both the forest (left) and plantation (right). The plots were generated with the geoR package in R, using least squares fit to the data. The plots demonstrate that all parameters contain very high nugget variance and a small range, indicating that the analysis were independent at distances <2 m, which renders most samples independent.

C.4 Best SEM models of the environmental factors on soil a) CO\textsubscript{2} and b) N\textsubscript{2}O fluxes on the plantation and c) CO\textsubscript{2} and d) N\textsubscript{2}O in the forest. Models were selected based on BIC and RSME values and addition of paths was decided based on the modification indices.
Values next to the arrows indicate the unstandardized coefficients and the width of the arrows indicates the statistical significance of the path (dotted line $P>0.5$, dashed line $0.2<P<0.5$, line $0.05<P<0.2$, thick line $0.01<P<0.05$, thicker line $P<0.01$, thickest lines $P<0.001$). The models suggest that the main drivers for CO$_2$ flux variability are ST and BD for both sites, whereas either ST (plantation) or WFPS (forest) are the main drivers for N$_2$O flux variability.

C.5 SEM diagrams like in figure 4 with the inclusion of biological parameters (biomass: a-d and tree growth rate: e-f) for the plantation (a and b) and the forest (c-f). Models were selected based on BIC and RSME values and addition of paths was decided based on the modification indices. Values next to the arrows indicate the unstandardized coefficients and the width of the arrows indicates the statistical significance of the path (dotted line $P>0.5$, dashed line $0.2<P<0.5$, line $0.05<P<0.2$, thick line $0.01<P<0.05$, thicker line $P<0.01$, thickest lines $P<0.001$). The models suggest that tree biomass has much greater influence on the soil gas fluxes in the forest than the plantation and that tree growth rate has a strong direct influence on soil N$_2$O fluxes in the forest.

D.1 Conceptual figure of the factors influencing forest growth rate and soil N$_2$O fluxes in tropical forests. The cartoon on the left outlines carbon flow from the atmosphere to soils. The small inset on the roots shows the main areas of carbon flow from root to the soil: root border cells (A), root hairs (B), and (C). The diagram on the right shows the main pathways of the nitrogen cycle. The green triangle denotes the processes that require labile carbon.

D.2 Exponential fit ($N_2O = 1.8_{1.3}^{2.2}*exp(1.8_{1.5}^{2.3}*Tree growth rate); \ R^2=0.7, n=33$) between monthly tree growth rates MgC ha$^{-1}$ month$^{-1}$ and soil N$_2$O fluxes from the km 67 eddy covariance tower site at the Tapajos National Forest, south of Santarem, Brazil. Monthly tree growth rates were obtained from dendrometry measurements on 1000 trees in four 4ha transects. Monthly soil N$_2$O fluxes were the geometric mean of 16 soil gas fluxes (two sampling dates, eight chambers each) from a 1 ha plot at the confluence of the transects.

D.3 Exponential relationship between overall forest growth rate (FGR) and a) wet season and b) annual soil N$_2$O flux in the Amazon basin. The symbols denote the different regions:
triangles = Tapajos National Forest, circles = Caxiuana national Forest, and squares= Manaus. Exponential fits to the data resulted in \( \text{N}_2\text{O} \) flux = \( 0.7^{1.3} \times \text{EXP}(\text{FGR}^{1.71.5^{1.9}}) \), \( P<0.0001, R^2 = 0.9, n=14 \), for the wet season data and \( \text{N}_2\text{O} \) flux = \( 2.8^{0.97\pm0.12} \times \text{EXP}(\text{FGR}^{0.97\pm0.12}) \), \( P<0.001, R^2 = 0.97, n=6 \). Although an exponential curve was the best fit to the data at hand, we expect that at higher tree wood growth rates soil \( \text{N}_2\text{O} \) fluxes reach a plateau when carbon is not limiting microorganisms, or potentially decrease when very fast growth increases tree competition for nutrients and limit the microbial activity.

D.4 Predicted Amazon basin wide forest soil \( \text{N}_2\text{O} \) fluxes, based on the RainFor plot database and our exponential fit between soil \( \text{N}_2\text{O} \) flux and forest tree growth rate. Color of dots indicates \( \text{N}_2\text{O} \) flux in kg-N ha\(^{-2}\) y\(^{-1}\); colors ranges are: blue 0.4-2.0, green, 2.0-2.5, yellow 2.5-3.2, oker 3.2-3.8, and red 3.8-12.6 kg-N ha\(^{-2}\) y\(^{-1}\). Note that predicted \( \text{N}_2\text{O} \) fluxes are highest in the western Amazon basin, the area where no wet season or annual soil \( \text{N}_2\text{O} \) flux measurements ever have been collected.

D.S.1 Depiction of our simple model for the influence of environmental parameters and tree growth on soil \( \text{N}_2\text{O} \) fluxes. The terms along the arrows indicate the driver/process behind the influence of the predictor variable on the response variable.

D.S.2 Structural Equation Model (SEM) analysis based on our monthly dataset from the Tapajos National Forest in Brazil supports that tree wood growth is a strong predictor for soil \( \text{N}_2\text{O} \) fluxes. The size of the arrows depicts the strength of the relationship, with the values indicating the unstandardized coefficients (slope of the relationship) and the superscript denotes the statistical significance of the path.
LIST OF TABLES

A.1 Multiple regression and correlation coefficients for mean daily and monthly fluxes for CO₂ and N₂O. The CO₂ fluxes were also broken down by season.................................83

B.1 Site characteristics and fluxes...........................................................................................................................................96

B.2 Species used for flux measurements.....................................................................................................................................................................................96

B.3 Slope direction, summed Akaike weight, adjusted correlation coefficients, and P-values for the multiple linear regressions by species for by-day corrected CO₂ fluxes and N₂O fluxes also after by-species correction.................................................................................................................100

B.4 Soil and flux measurements adjacent to three tree species with differing N₂O fluxes.....................................................................................................................................................................................100

C.1 Site locations and mean soil properties and gas fluxes (letters denote significant difference P<0.01, within columns)......................................................................................................................................................................141

C.2 Species used for flux measurements.................................................................................................................................................................................................142

C.3 Vegetation mass and carbon equivalent* fluxes from plantation and forest.................143

C.4 Fraction of flux variance explained by species and soil variables.........................................144

C.5 Effects of legume tree species on soil parameters on the plantation and in the forest.........................................................................................................................................................................................145

D.1 Annual measured and model predicted wood growth (Mg-C ha⁻¹ y⁻¹) and N₂O flux (kg-N ha⁻¹ y⁻¹) for a clay-rich and sandy site in the Tapajos National Forest, Brazil...........175
ABSTRACT

This thesis presents data collected and analyzed to determine the influence of above ground biological factors on the spatial and temporal variability of tropical soil biogeochemical processes. The tropics are the largest natural source of CO$_2$ and N$_2$O to the atmosphere and many tropical forests are changing due to climate or land-use change and forest fragmentation. To understand how these changes are affecting ecosystem feedbacks to climate change we need to understand the plant-soil interactions in tropical forests and how these scale to the whole forest and region. For this thesis, I completed four studies that investigated the interaction of the tree species and forest growth with soil trace gas fluxes within the Amazon basin.

Locally, tree species do influence soil N$_2$O fluxes, with fluxes close to four out of fifteen tree species consistently elevated above the overall mean and consistently low near two species. These results suggest that tree species composition can significantly influence soil biogeochemistry. Experimental sugar additions elevated N$_2$O fluxes, suggesting that N$_2$O cycling is mostly driven by heterotrophic (carbon-limited) denitrifiers, and that carbon transport into the soil by trees may present a mechanism for the observed differences. Alternatively, tree-soil competition for nutrients could explain the tree species related soil N$_2$O flux differences. However, soil nitrate concentrations and low N$_2$O fluxes associated with legumes, suggest that nitrogen is not limiting. This work provides evidence that vegetation species composition can be a
controlling factor in overall trace gas emissions in tropical forests, although I found that only rather large (20%) change in species composition would cause an appreciable effect on the landscape-scale forest soil gas flux.

In order to better isolate the effects of species on soil processes, I also investigated soil gas fluxes in a tropical plantation, where trees were grown in monoculture plots. As in the natural forest, different tree species were associated with flux differences, though the species N$_2$O flux rank order was unlike what I found in the forest, indicating that monoculture plantation plots are not generally informative for species influence on soil processes in diverse forests. Fast tree growth rates and overall lower fluxes of CO$_2$ and N$_2$O from plantation vs. natural forest or agricultural soils suggest that conversion of abandoned farmland to plantation may reduce greenhouse gas fluxes to the atmosphere in tropical systems, a net benefit from a climate change policy perspective.

Finally, motivated by the finding that tree carbon export may influence N$_2$O gas production in soils at the local scale, I investigated the effect of variation in growth rates of forest stands on regional variations in N$_2$O production. I found that site-to-site and monthly flux variability within the Tapajos National Forest (south of Santarem, Brazil) and across the central-eastern Amazon basin is significantly and positively correlated with forest growth rates. I hypothesize that this relationship is a consequence of: (1) the dominance of denitrification (as opposed to nitrification) in driving N$_2$O emissions in
wet, clay-rich tropical soils that are conducive to anaerobic metabolism (especially in wet seasons); (2) the requirement of denitrifiers, as obligatory heterotrophs, for labile carbon, which is limited in tropical soil, and (3) the fact that downward sap flow in trees is the main source of carbon for both stem growth and root exudation. The plausibility of this hypothesis is supported by results from a process-based, numerical model (PnET-DNDC), which, when trained to climatic and ecological data of our sites, reproduces the wood growth and soil N₂O flux patterns we observed. Extrapolating the regionally observed correlation between stand-level tree growth and N₂O fluxes, to the Amazon basin as a whole using wood growth measurements from forest inventory plots, yields a mean soil N₂O flux of 2.6 kg-N ha⁻¹ y⁻¹ for the whole Amazon basin, higher than most previously published estimates. This suggests that tropical forests may be a bigger contributor to global N₂O budget than previously thought, a consequence of accounting for the importance of processes that link vegetation carbon dynamics to soil biogeochemistry.
INTRODUCTION

1.1 Context of Research

Spatial and temporal variability of soil gas fluxes is much-studied, but remains an interesting and elusive problem for biogeochemists. Recent papers (Werner, Butterbach-Bahl et al. 2007; Groffman, Butterbach-Bahl et al. 2009) have shown that we still have poor understanding of local and time-separated forces acting on soil gas fluxes. Soil gas fluxes are the net result of production, consumption, and transport processes within the soil and litter layer (Smith, Ball et al. 2003). Gas production and consumption depend on precipitation variability and changes in substrate availability, which in turn depend on the supply of labile carbon to microorganisms by plants and competition for nutrients between microorganisms and plants. A better understanding of the spatial and temporal variability of soil gas fluxes will help to predict future responses of natural ecosystems to climate change and how we potentially can mitigate some of these fluxes.

The greenhouse gases (GHG) methane (CH₄), carbon dioxide (CO₂), and nitrous oxide (N₂O), all are actively produced or consumed by bacteria in soils, which leads to the gas fluxes across the soil-atmosphere interface. Once in the atmosphere these gases contribute to climate change by trapping heat in the atmosphere (IPCC 2007) and N₂O also is an important contributor to ozone destruction in the stratosphere through the reaction with UV light which produces NO—a catalyst of ozone destruction (Crutzen 1970). A recent study has shown that N₂O has become the dominant force in ozone
destruction since the Montreal Protocol has reduced CFC production (Ravishankara, Daniel et al. 2009). Since the onset of the industrial revolution atmospheric CH$_4$, CO$_2$, and N$_2$O concentrations have increased exponentially (IPCC 2007). Although most of this increase is due to human activity, a large part of the global cycling of these gases resides within natural ecosystems.

Tropical forests are of particular interest with regards to soil CH$_4$, CO$_2$, and N$_2$O fluxes, because all these are microbially mediated and the microbial activity in tropical ecosystems is very high. The soil CO$_2$ emissions of tropical forests are considered to be the largest of any terrestrial ecosystem (Raich and Schlesinger 1992), representing approximately 20% of all naturally produced CO$_2$. Contribution of tropical forest ecosystems to the overall N$_2$O budget is even larger, and is estimated at ~20% of all global N$_2$O production (Matson and Vitousek 1990; Bouwman, Fung et al. 1993; Werner, Butterbach-Bahl et al. 2007). It is therefore very surprising that soil CO$_2$ and N$_2$O fluxes have only been measured at a handful of locations around the Amazon basin. This level of coverage is woefully insufficient to determine overall soil CO$_2$ and N$_2$O fluxes of the Amazon basin or the global tropics. To increase our understanding of tropical soil gas fluxes, our approach needs to include knowledge of spatial and temporal variability – annual variability of precipitation has a strong influence on soil gas fluxes at each site (Butterbach-Bahl, Kock et al. 2004) and soil texture has a strong influence on soil gas fluxes (Keller, Varner et al. 2005)- and how they relate to soil and ecosystem properties.
Modeling of ecosystem processes provides an alternative method to determine the soil greenhouse gas fluxes in ecosystems that have not been extensively measured. Both simple and complex modeling approaches have been advocated, ranging from simple correlation of soil N$_2$O flux with ecosystem CO$_2$ exchange (Garcia-Montiel, Melillo et al. 2002) and with litter carbon-to-nitrogen ratio (Klemedtsson, von Arnold et al. 2005) to more complex ecosystem models such as TEM (Melillo, Steudler et al. 2001), DAYCENT (Del Grosso, Mosier et al. 2005) and PnET-DNDC (Li, Aber et al. 2000). The simpler models have the advantage that the link between the predictor and response variable is immediate, though they are generally based on empirical studies, without a clear understanding of the underlying processes. For instance, the relationship between soil N$_2$O and ecosystem CO$_2$ flux was derived in forests and pastures in Rondonia, southern Brazil (Garcia-Montiel, Melillo et al. 2002). Soils at their sampling locations are generally Ultisols (sandy highly weathered soils), where the majority of N$_2$O production occurs through nitrification. Since nitrification is strongly tied to mineralization, the CO$_2$ and N$_2$O flux can be correlated, though CO$_2$ fluxes are a thousand times greater than the N$_2$O fluxes. When denitrification contributes significantly to soil N$_2$O fluxes, mainly in clay-rich soils during the wet season (Keller, Varner et al. 2005), this relationship breaks down due to the near 1:1 ratio of N$_2$O and CO$_2$ production during denitrification (Burford and Bremner 1975). The complex models are more flexible and incorporate many detailed ecosystem processes. However, model complexity can lead to loss of causality. Furthermore, the model complexity often creates instability of the model
when input parameters are changed and optimization of model parameters not necessarily leads to changes in model behavior and output. Comparison of the different models often find large variability in model predictions on a regional scale (Melillo, Steudler et al. 2001; Werner, Butterbach-Bahl et al. 2007).

1.2 Statement of the objectives

For my thesis research, I set out to determine how trees and aboveground biomass influence soil greenhouse gas production and the spatial and temporal variability of the resulting gas fluxes. My objective was to determine whether plant species influenced soil CO$_2$ and N$_2$O fluxes in diverse, complex tropical forests, with a focus on the wet season when denitrification and soil N$_2$O fluxes were expected to be the greatest. This research is presented in Appendix B. Unlike this research, most previous studies investigating the influence of tree species on soil parameters and processes used monoculture plantations (Binkley and Menyailo 2005). The presence of a local plantation near to the forest allowed me to investigate the differences between natural diverse forests diversity and monoculture plantation forests in how they influence soil processes (Appendix C). I collaborated with Drs. Michael Keller, Patrick Crill, Cosme de Oliveira and Ruth Varner to obtain access to soil gas flux data they collected using both manual and automated methods. Appendix A details the research and addresses the relative importance of spatial and temporal flux variability on overall annual flux
estimates. Lastly, the knowledge of spatial soil N₂O flux variability within the forest that could not be explained by precipitation nor soil textural differences led me to pursue the objective to determine Amazon basin wide soil N₂O fluxes based on published wood growth rates (Malhi, Baker et al. 2004; Anderson, Malhi et al. 2009). The influence of site averaged tree growth on soil N₂O fluxes was determined on a monthly, seasonal, and annual timescale at our core sites in the Tapajos National Forest, Caxiuana, and Manaus. This research is presented in Appendix D.
PRESENT STUDY

For my thesis I specifically looked at the influence of vegetation on spatial and temporal variability in tropical ecosystems, where previous work has shown that soil CO$_2$ and N$_2$O fluxes are amongst the highest globally (Matson and Vitousek 1990; Raich and Schlesinger 1992; Bouwman, Fung et al. 1993). The approach was to measure soil gas fluxes and soil parameters, generally used in biogeochemical models, to determine how well these parameters did to explain the fluxes. I coupled these measurements and autochamber measurements with the climate, eddy covariance and forest demography measurements taken at the km 67 tower (Saleska, Miller et al. 2003). Both four years of repeated flux measurements and automated flux measurements over three and a half years for CO$_2$ and eight months for N$_2$O, could be coupled with light, precipitation, temperature, carbon exchange, tree growth data to determine what were the main drivers for the temporal flux variability on a daily and monthly time-scales.

Vegetation is the main source of carbon to soil microorganisms responsible for the soil gas production. Several experiments have shown that tropical forest soils can be severely carbon limited (Nobre, Keller et al. 2001; Garcia-Montiel, Melillo et al. 2003), carbon which mainly comes from plant derived leaf and root litter and root exudates. My previous research on the spatial and temporal variability of soil CO$_2$ and N$_2$O fluxes at Biosphere 2 (van Haren, Handley et al. 2005), revealed that precipitation was the main cause for temporal variability of soil CO$_2$ and N$_2$O fluxes, but that spatial differences were consistent throughout time. The spatial variability appeared to be tied
to the presence of certain tree species (*Arrenga pinnata* or sugar palm and *Pterocarpus indicus*, a legume species), but poor spatial replication of tree species made it impossible to definitively state that the spatial variability was tied to tree species. This work led me to ask the question: do plant species influence soil properties and microbial communities in predictable ways both in forests and monoculture plantations? The within-site result that tree species can influence soil N$_2$O fluxes and that N$_2$O fluxes appear to be negatively correlated with tree growth rates, I further investigated on the plot level scale at different forests within the Amazon basin. The results obtained in this study showed that forest growth rate and soil N$_2$O fluxes are highly correlated both at local and Pan Amazonia scales. This suggests that the coupling between soil N$_2$O fluxes and forest growth rate in tropical ecosystems is much tighter than previously envisioned. This relationship is based on the facts that 1) vegetation is the main source of carbon to soil microbes and 2) soil microbes are generally carbon limited in tropical ecosystems (Nobre, Keller et al. 2001; Garcia-Montiel, Melillo et al. 2003).

Since I set out to determine the relative importance of multiple variables on soil gas fluxes, I delved into the statistical technique of Structural Equation Modeling (SEM). Unlike all other regression analysis, SEM was developed to explain the overall covariation pattern of group of continuous variables. It requires the a-priori development of one or several models based on cause-and-effect relationships, which then can be tested with statistically robust measures, such as the Aikake Information Criterion (Johnson and Omland 2004). SEM modeling can both be used as a
confirmatory and exploratory tool, though in the latter mode, only multiple a-priori models or the inclusion of certain a-priori variables can be tested (Tomer and Pugesek 2003). The a-priory models I developed based on basic physical principles and tree ring growth analysis (Fritts 1976). The models were generally kept as simple as possible, to minimize potential model instability.

2.1 Summary of paper 1: Spatial and temporal variability of soil CO$_2$ and N$_2$O fluxes in a clay-rich site in the Tapajos National Forest, east-central Amazonia, Brazil.

Spatially and temporally extensive soil gas flux data, in combination with environmental, tree inventory plot and phenological data, can lead to a greater understanding in the main drivers and potential mechanisms of soil gas flux variability. Spatial and temporal explicit soil gas fluxes at a single site can also provide important insights into strategic sampling design. Most studies either sample soil gas fluxes manually (8-24 locations), repeating the measurements within the same plot on a bi-monthly or monthly basis, or automatically with a small number of chambers (less than 10). Notable exceptions include a study of the spatial and temporal variability of soil N$_2$O fluxes in Queensland Australia (Breuer, Papen et al. 2000) and of soil CO$_2$ fluxes in Harvard forest (Savage and Davidson 2003). In our study we compiled soil gas fluxes from a three tiered system: 1) high spatial distribution with ~ 200 manual chamber locations within 20 ha of forest plots sampled during the wet season only, 2) 1 ha spatially distributed, monthly repeated manual soil gas measurements with up to 24
chambers, and 3) automated chamber measurements with eight chambers in ~0.5 ha. This study increased both the spatial and temporal extend to which a single site has been studied. The three sampling methods were not all conducted at the same time, which is why we compared fluxes from the three sampling schemes collected during times of the year with similar climatic conditions, i.e., wet or dry season. We applied a bootstrap resampling technique to ensure that differences in statistical properties of the datasets were not caused by differences in sampling frequency. Structural Equation Modeling (SEM) was used to determine the relative importance of climatic and phenological parameters on soil CO₂ and N₂O gas fluxes. We acquired the PnET-DNDC (Li, Aber et al. 2000) and ForestDNDCtropica (Kiese, Li et al. 2005) models, which have two different aboveground formulations, but the same belowground biogeochemical characterizations, to determine whether either of these models could reproduce the observed temporal or spatial variability. The primary conclusions of this work are:

- Automated chambers that are installed into the soil surface appear to underestimate the soil CO₂ and N₂O fluxes by 36 and 70%, respectively.

How to measure a gas flux across the soil-atmosphere interface has remained an ongoing debate in the biogeochemistry community. Recent papers have detailed the importance of chamber methods (Rochette and Eriksen-Hamel 2008) and insertion depth of the chamber base (Matson, Vitousek et al. 1990; Heinemeyer, Di Bene et al. 2011) for the evaluation of soil gas flux measurements. Especially the insertion depth can have strong implications for both short term and long term flux dynamics: cutting of
roots leads to short-term flux increases, but absence of roots leads to long-term decreases. The latter has also been documented in trenching experiments (Silver, Thompson et al. 2005). The short-term installation of our manual chambers – fluxes were measured within an hour of installation – did not impact soil gas fluxes, but the long-term installation of the automated chambers, did lead to a reduction of both soil CO$_2$ and N$_2$O fluxes, most likely due to a reduction in fine root content.

- Spatial variability of soil N$_2$O fluxes is greater than CO$_2$ fluxes, while both fluxes are greatly influenced by the changes in precipitation.

Our spatial design was influenced by the selection of tree species, since the species only appeared to have influence on the soil N$_2$O fluxes (see Appendix B), the spatial N$_2$O flux variability was twice the CO$_2$ flux variability (coefficient of variance was 75 and 37, respectively). A second outcome of our spatial sampling design was that the spatial CO$_2$ fluxes were 20% higher than the manual repeated chamber measurements. Approximately the same difference was found for the CO$_2$ fluxes close to and far from large trees, which suggests that our spatial sampling mean represents an overestimation. Mean N$_2$O flux estimates were not affected since higher and lower tree species means canceled each other out. Manual and automated chamber measurements from the wet season were 3 times the dry season fluxes. The change in fluxes was corroborated by the model runs, though these gave much lower fluxes during the dry season, which is most likely due to the shallow parameterization of the model soil.
• Monthly N\textsubscript{2}O flux variability is most strongly correlated with tree growth rates, which suggests that at minimum these two factors are strongly correlated.

The monthly manually collected soil N\textsubscript{2}O fluxes were most strongly correlated with tree growth rates, both in our linear regression models (R2 values) and SEM modeling (R2 values). Our SEM model was based on Fritts (1976), who developed a model for the interaction between climate and tree-ring width. We simplified the model to reduce the amount of paths, which reduce the stability of the model, since we only had a limited amount of data (33 months). The strongest factor directly influencing soil N\textsubscript{2}O fluxes was the tree growth rate, then soil moisture (WFPS), and soil temperature was not significant. Most often soil N\textsubscript{2}O fluxes have been correlated both with soil CO\textsubscript{2}, litter deposition, and C-to-N ratios, all of which are both an indication of mineralization rates. Litter deposition was mainly driven by a strong increase in litter-fall during the early dry season, and thus strongly anti-correlated with soil N\textsubscript{2}O fluxes. Although, the correlation between soil N\textsubscript{2}O fluxes and tree growth rate does not imply causality, there are several hypotheses that can be tested to explain the correlation.

• The models can predict the general annual variability, but they appear to greatly overestimate the responsiveness of the soil community to precipitation events.

The temporal model calculations, which were comparable for both models, appeared to be more responsive to precipitation variability than the measured manual and automated fluxes. This over-prediction of model responsiveness to precipitation and soil moisture could be the result of the shallow soil parameterization (0.3 m), which
excludes a deeper soil gas reservoir for diffusive gas fluxes. (Davidson, Ishida et al. 2004) found that maximum N₂O production occurred at 0.3 m depth, whereas CO₂ production occurred meters deep in the soil. Gas diffusion from depth can moderate soil gas flux variability over time scales of days rather than weeks or months (van Haren, Handley et al. 2005), which means that model underestimation of soil gas fluxes during the dry season are likely the result of shallow soil. Alternatively, the difference between the model and automated chamber means is an artifact of averaging the chamber data. Individual chamber fluxes are temporally more similar to the model results, which to me indicated that the temporal variability is quite heterogeneous from chamber to chamber.

Statement of contribution
Joost van Haren, the candidate, collected the data for the spatial analysis, conducted the overall data and statistical analysis, and initiated and completed most of the writing. The candidate conducted the modeling with the generous help of Drs. Werner (ForestDNDC Tropica) and Frolking and Li (PnET-DNDC). Suggestions of Drs. Saleska, Varner, Crill, Li, and Frolking improved the writing and data analysis.
2.2 Summary of paper 2: Do plant species influence soil CO$_2$ and N$_2$O fluxes in a diverse tropical forest.

In three clay-rich sites within the Tapajos National Forest, I measured the soil CO$_2$ and N$_2$O fluxes close to and far away from large trees from 15 different tree species. The three sites were all part of the forest inventory work that was initiated by Dr. Steve Wofsy of Harvard University and the total forest area covered was 20 ha. These sites contained long transects, where all trees greater than >10 cm in diameter at breast height (DBH) were measured in one fifth of the transect and >35 cm DBH were measured throughout. Besides soil gas fluxes, I measured the soil components that were predicted (Breuer, Papen et al. 2000; Davidson and Verchot 2000; Kiese, Li et al. 2005) to be most important for soil gas flux variability: bulk density, moisture content, pH, and temperature. We further measured nitrate concentration, root density, microbial biomass, and response to sugar addition close to three tree species that were most consistently different from each other. All the fluxes measurements were conducted during the wet seasons of 2005, 2006, and 2007, since we expected the flux variability to be higher during the wet season (Keller, Varner et al. 2005). After the collection of the soil gas fluxes, I revisited all the sites and measured all trees >1 cm DBH within a 3 m radius of the flux location. We used multiple linear regression in combination with the Akaike Information Criterion (AIC) to determine the best regression model for the data with the measured variables. The main conclusions of this paper were:
Soil CO₂ fluxes were not influenced by tree species and best (only 23%) explained by a regression model of bulk density, temperature and liana mass present.

Although soil CO₂ fluxes varied between 39 and 769 mg-C m⁻² h⁻¹, this variability was not caused by tree species identity. Presence of large trees, did have a significant effect on soil CO₂ fluxes, which was reduced far from large trees. We postulated that this was mainly due to reduced root densities, reflected in the higher soil bulk density away from large trees. Multiple linear regression analysis revealed that 23% of all CO₂ flux variability could be explained by a soil bulk density, temperature, and the liana mass present. Greater liana densities in forests have been predicted with climate change associated increasing drought and temperature (Phillips, Lewis et al. 2008). The liana soil CO₂ flux relationship could therefore represent a positive feedback to climate change.

Tree species did influence soil N₂O fluxes and explained most of the observed flux variance, most likely through differential carbon limitation of soil microorganisms.

Of the 15 tree species measured three species stood out with either high (*Caryocar villosum*) or low (*Erisma uncinnatum* and *Vochysia maxima*, both Vochysiaceae) soil N₂O fluxes. We conducted more detailed sampling close to these species to determine how these species influence the soil N₂O flux. We observed no difference in fine root content, microbial biomass, C-to-N ratio, or nitrate concentration, but found that after addition of sugar soils close to *Caryocar villosum* responded with much higher N₂O
fluxes than the Vochysiaceae. We interpret these results that the difference in soil N\textsubscript{2}O flux between these species is caused by a difference in belowground carbon flux.

- Tree species associated differences in soil N\textsubscript{2}O fluxes only could significantly affect the overall forest ecosystem flux if species changes of 20% occur in overall forest composition.

Because we conducted the sampling within 20 ha, we combined the species flux data and applied it to an Arc-GIS spatial database with all the tree species, unmeasured species were assigned the overall mean N\textsubscript{2}O flux and each tree was assigned a sphere of influence (Zinke 1962) that was proportional to the stem diameter of the tree. Initially we calculated a species weighted mean for the whole transect area, which was indistinguishable from the overall mean. We then modified the unknown species proportion to either the low or high flux species to assess how much the species composition would have to change to cause measureable differences in the overall N\textsubscript{2}O flux. This value was \(~20\%\), a forest composition change that is unlikely to happen over the short-term during climate change.

- Tree growth rate appears to negatively affect the soil N\textsubscript{2}O flux, whereas carbon addition to the soil positively affected soil CO\textsubscript{2} and N\textsubscript{2}O fluxes.

We found a strong negative correlation between the species mean N\textsubscript{2}O flux and tree growth rate, which had correlation coefficient comparable to N\textsubscript{2}O flux and soil moisture
(R² of 0.65 vs. 0.7). Multiple regression of the two variables decreased the Aikake Information Criterium, which suggests that there was some interaction between the two predictor variables. The negative relationship between soil N₂O flux and tree growth rate can mean that faster growing tree species either need more nutrients or allocate less carbon below ground. The former leads to more plant competition with the belowground microorganisms for the substrates to nitrification and denitrification. The latter, under constant nutrient conditions of a site, leads to reduced root turnover and exudation.

Statement of contribution

Joost van Haren, the candidate, collected the data for the study, conducted the overall data and statistical analysis, and initiated and completed most of the writing. Dr. Saleska advised during the spatial sampling method development and without his suggestion we would not have measured all the plant species close to the soil flux location. Dr. Hutyra provided data for the tree growth analysis and Dr. Restrepo provided the GIS analysis. Suggestions of Drs. Saleska, Keller, and Restrepo improved the writing and some of the data analysis.
2.3 Summary of paper 3: Tropical tree species effects on soil properties and greenhouse gas fluxes in monoculture and diverse forests.

In ecology and forestry experiments trees are planted in mixed or mono culture to determine the effect of each species on soil properties (Binkley and Menyailo 2005). Although monocultures are probably going to yield a stronger signal from the species of interest –without the interference of other species growing nearby-, the question remains: how relevant are monoculture plot results to diverse forest? Of the 15 selected species we measured in the forest, we managed to find nine on a nearby plantation in the township of Belterra – the location of one of the former Henry Ford rubber plantations. To increase our replication of legume plots, we further selected one legume species (three total on four plots) on the plantation that was poorly represented in the forest. The plantation was planted between 1979 and 1981 by EMBRAPA (the Brazilian USDA) and was the only plantation that remained in workable condition in the region. I initially hoped to use a former plantation, which had been used for tree species related analysis of carbon, litter, and nutrient dynamics (Smith, Gholz et al. 1998). The plantation developed by SUDAM at Curua-una (~30 km to the east) in the late 1950s was to my regret abandoned in the late 1990s and suffered fire and blowdown damage, which rendered this plantation unusable. We conducted the same flux and ancilliary measurements on the plantation as in the forest, except for the stem diameter and species of all trees >1 cm DBH within 3m of the flux location. We did measure the DBH of all the trees on the same monoculture plot, the size of the plot, and
the distance of each flux location relative to the trees and flux locations. Based on the stem measurements we calculated total biomass and annual growth of the trees. We used spatial statistics (semi-variograms constructed and analyzed with the geoR package in R statistical software) to determine the spatial independence of samples within monoculture tree plots. To determine the relative importance of species and soil parameters we developed a simple model for path analysis, which is a statistical regression analysis that accounts for the covariance between the different predictor variables. The main conclusions of this paper are:

- Tree species did influence soil CO$_2$ and N$_2$O fluxes on the plantation, however, species rank N$_2$O fluxes on the plantation and in the forest suggest that monocultures have little predictive capability for species specific plant-soil interactions in diverse forests.

Both soil CO$_2$ and N$_2$O fluxes were species specific on the monoculture plantation. Although, only three of the tree species were replicated on the plantation, the semi-variogram analysis indicated that, except for soil moisture, samples were independent even on the plot scale (<5 m). Therefore we could treat the multiple samples within one plot as replicates and the observed species differences are real. That said, the relationship between the species differences, especially N$_2$O fluxes, for which we have significant differences in both tree ecosystems, does not match between the two locations. This confirms the trend found on mono and mixed culture plantations, where
the CO₂ flux differences found on monocultures were not present anymore on plots with mixtures of 3 or 6 of the same species (Murphy, Balser et al. 2008).

- Legume species can have a positive effect on the overall carbon balance even in monocultures.

To my surprise, soil N₂O fluxes associated with legumes on the plantation were consistently the lowest measured. Due to their capability to form symbiotic relationships with rhizobia, legumes have always been considered nitrogen sufficient and thus can lead to greater soil N₂O fluxes around them (Erickson, Keller et al. 2001; Hall and Asner 2007; Arai, Ishizuka et al. 2008). In old terra firme forests – trees in the Tapajos National Forest can be >500 years old (Vieira, Trumbore et al. 2005), it is common that legumes are not nodulated since these forests are not limited in nitrogen (Ometto, Ehleringer et al. 2006) and nitrogen fixation is a carbon and phosphorous expensive process (Davidson 2008). However, in nutrient poor soils, such as impoverished farmland one would expect legumes to be nodulated, and all legume species within the plantation were (confirmed through visual inspection). At this point I can only provide two potential hypothesis for this surprising finding: 1) the microbial communities under legumes on this plantation were carbon starved, because the legume root exuded little carbon due to the strong allocation to stem growth and use of carbon in nitrogen fixation, alternatively 2) the legume species had poor water use
efficiency and disproportionately dried the soil underneath them and thus reducing the potential for denitrification, even in the wet season.

- When planted on old or abandoned agricultural land monocultures can provide strong greenhouse gas sequestration benefits on a 40 to 80 year rotation scheme, due to strong rapid growth during the first 20-30 years and slow recovery of the CO$_2$ and N$_2$O gas fluxes.

Although we only measured the growth, biomass and greenhouse gas fluxes on a single ~30 year old plantation, our growth and biomass results suggest that the tree species on this plantation were growing fast and that soil CO$_2$ and N$_2$O gas fluxes were still ~30 and 50% lower than in the neighboring forest on the same soil. Furthermore, the maximum annual soil CH$_4$ and N$_2$O fluxes, when calculated from the wet season fluxes and thus representing a maximum possible flux and on a similar scale as the tree biomass and growth (Mg-C ha$^{-1}$ y$^{-1}$; CH$_4$ and N$_2$O flux equivalents were calculated based on their 100 year time horizon global warming potential relative to CO$_2$ of 25 and 298, respectively (IPCC 2007)), were negligible (<1% of the total carbon stored above ground) to the overall greenhouse gas balance of the plantation. Maximum annual CO$_2$ fluxes ranged from 5-30% of the plot biomass, which is substantial though most of this carbon released was respiring from litter and roots (both representing ~60% of the total soil respiration flux).
Statement of contribution

Joost van Haren, the candidate, collected the data for the study, conducted the overall data and statistical analysis, and initiated and completed most of the writing. Suggestions of Drs. Saleska, Keller, and Oliveira improved the writing and some of the data analysis.

2.4 Summary of paper 4: Forest growth rate predicts tropical soil N$_2$O fluxes.

In the previous chapters I mainly focused on the site based variability of soil gas fluxes. In order to increase the level of inference of these studies, I measured the soil gas fluxes at four sites within the Tapajos National Forest (TNF), at four sites within the Caxiuana National Forest at the confluence of the Xingu and Amazon rivers, and three sites within Reserva Ducke in Manaus. Especially within the TNF, I found that soil textural differences could not explain the site-to-site variability. Keller, Varner, et al. (2005) found that overall soil gas fluxes were lower on sandy than clay-rich soils and that these differences were more pronounced during the wet season, presumably due to the higher air and water permeability of the sandier soils. However, within the TNF clay-rich soils had as much soil N$_2$O variability as across the soil textural classes. Since all the sites have long-term records of forest dynamics and growth, I compared the overall mass growth rate at the sites with the soil N$_2$O flux, which led to the hypothesis: soil N$_2$O fluxes and tree growth rates are covariates driven by soil fertility and precipitation.
We extrapolated the relationship between soil $\text{N}_2\text{O}$ fluxes and wood growth rates to the overall Amazon basin using the regional analysis of the Rainfor plot database ([Malhi, Baker et al. 2004; Anderson, Malhi et al. 2009] >110 plots around the Amazon basin). Although, wood growth measurements are not without their problems (Clark and Clark 1999; Clark, Brown et al. 2001), these measurements could provide a simple method to scale up soil $\text{N}_2\text{O}$ fluxes from forest plots to larger regions. The main conclusions of this chapter are:

- Across the central and eastern Amazon basin soil $\text{N}_2\text{O}$ fluxes are positively correlated with forest wood growth rates.

  I constructed an exponential regression curve ($R^2 =0.89$, $P<0.0001$, $n = 14$) between forest growth rate from four sites within the TNF and Caxiuana National Forest and three from Reserva Ducka close to Manausd soil $\text{N}_2\text{O}$ fluxes from, all taken during the mid to late wet season. From the literature (Luizao, Matson et al. 1989; Davidson, Ishida et al. 2004; Keller, Varner et al. 2005) I found only three papers focused on locations within the Amazon basin where annual soil gas fluxes and tree demographic measurements were taken at the same time. The trend between annual soil $\text{N}_2\text{O}$ fluxes and annual tree growth was also highly significant ($R^2 =0.95$, $P<0.005$, $n = 7$), though with a much lower slope. These results indicate that forest growth and soil $\text{N}_2\text{O}$ fluxes are strongly correlated, which is not surprising since both are strongly influenced by precipitation and soil fertility. Three, not mutually exclusive, mechanisms can explain
this covariance: 1) with increased precipitation tree within a forest invest more carbon to stem growth and roots, because higher water availability enables more sap transport out of the canopy, 2) through their roots trees stimulate the soil microbial community by adding labile carbon and especially denitrification – an obligatory heterotrophic process can become more abundant, and 3) within a forest on more fertile soil nutrient competition between trees and microbes is less intense than in forests on poor soils, with reduced nutrient competition soil microbes have more substrate available for nitrification and denitrification.

- Within site flux variability is comparable to the overall Amazon basin N₂O flux variability.

We used data from the multiple forest plots within a single local site from the Rainfor plot database ((Malhi, Baker et al. 2004; Anderson, Malhi et al. 2009) >110 plots around the Amazon basin) to assess the relative importance of regional over local forest soil N₂O flux variability. Though overall higher soil N₂O fluxes are predicted for the western Amazon basin, the wood growth and therefore predicted N₂O flux variability within site also increases. This can be explained by considering both precipitation and soil texture as main drivers for both wood growth and soil N₂O fluxes.

- Our prediction for the Amazon basin wide soil N₂O flux falls at the high end of published N₂O flux estimates.
Basin wide estimates of soil N\textsubscript{2}O fluxes have been made since the early 1990s (Matson and Vitousek 1990) and have used simple up-scaling techniques or more complicated terrestrial modeling approaches (Potter, Davidson et al. 1998; Melillo, Steudler et al. 2001; Werner, Butterbach-Bahl et al. 2007). Published basin wide average flux estimates range from 1.1-2.6 kg-N ha\textsuperscript{-1} y\textsuperscript{-1}. Our estimate of 2.5-3.0 kg-N ha\textsuperscript{-1} y\textsuperscript{-1} (95% CI) is on the high side of this range. No significant change was found when we used the (Potter, Davidson et al. 1998) soil areas to scale up the N\textsubscript{2}O flux by soil type 2.6-2.9 kg-N ha\textsuperscript{-1} y\textsuperscript{-1} (95% CI). The discrepancy between our results and Potter et al. could be because the mean wood growth estimate for the Amazon basin based on (Malhi, Baker et al. 2004; Anderson, Malhi et al. 2009) was 2.4 Mg-C ha\textsuperscript{-1} y\textsuperscript{-1}, which is substantially higher than the Net Primary Productivity (NPP) estimate from Potter, Davidson et al. (Potter, Davidson et al. 1998): 1.4 Mg-C ha\textsuperscript{-1} y\textsuperscript{-1}. Plot selection bias could potentially explain the difference, though it appears that the NPP in the Potter et al. model was strongly limited by light, and therefore yielded higher NPP rates in the eastern-central Amazon basin, in contrast to the Terrestrial Ecosystem Model (Melillo, Steudler et al. 2001) and the plot based ground measurements, who both put the highest productivity in the western Amazon basin. These discrepancies highlight the continued need for both wider scale ground based measurement and model improvements.
• The current versions of the Forest DNDCTropica and PnETDNDC models do not resolve the potential mechanism behind the relationship between forest growth and soil N$_2$O fluxes.

With the help of Drs. Steve Frolking and Changshen Li, I started model runs with the PnET-DNDC model to determine whether I could test the precipitation and soil fertility hypotheses developed based on the correlation between the soil N$_2$O flux and forest growth rate. To my regret these model runs have not been conclusive as of yet. The ForestDNDCTropica model appeared to run well for the Tapajos forest site, it captured the temporal variability within the site (see Appendix A), though it did not capture the seasonality in growth, nor the total annual growth (1.2 vs measured: ~3.0 Mg-C ha$^{-1}$ y$^{-1}$). Soil texture change, from clay-rich to sandy (90 vs 9% clay) did change the magnitude of the soil N$_2$O flux appropriately, but not reduce the wood growth as expected. The PnET-DNDC model appears to capture both the wood growth and soil N$_2$O flux dynamics, though the wood growth is slightly overestimated at 3.8 Mg-C ha$^{-1}$ y$^{-1}$. Both on an annual and daily basis the wood growth correlates with the soil N$_2$O flux. However, respiration is overestimated by a factor of 2 to 3, which suggests that the model needs further calibration. Due to the problems with calibration of the model, I did not compare sites with different soil texture yet. The modeling component remains a work in progress, though it appears that comparison of these two models might lead to a better insight into the mechanism between forest growth and soil N$_2$O fluxes.
Statement of contribution

Joost van Haren, the candidate, collected the data for the study, conducted the overall data, modeling, and statistical analysis, and initiated and completed most of the writing. Drs. Li and Frolking provided support for the modeling effort. Forest inventory data from Caxiuana and Manaus were provided by Drs. Galbraith, Costa, and Castilho. Suggestions of Drs. Saleska and Oliveira improved the writing and some of the data analysis.

2.5 Summary and Conclusions of this Doctoral Research Program

The research presented here, provides the first assessment of how ecology and tree species identity can influence soil biogeochemistry in diverse tropical forests. It adds to the existing literature though analysis of the influence of tree species on soil gas fluxes and the realization that trees through their roots can strongly influence soil N$_2$O fluxes. This led to the potential of combining overall forest growth with soil N$_2$O fluxes as a simple approach to scale up soil chamber flux measurements. The simple model should contribute to further work with detailed process models, which when properly calibrated should yield more precise estimates of regional flux variability, though the models will need to include deeper soil layers to capture the dry season diffusive soil gas flux.
The reader may notice an apparent paradox between the observation that species-specific growth rates are negatively correlated with soil N$_2$O emission within a forest stem (Appendix B), and the observation that the stand level growth rates are positively correlated with soil N$_2$O emissions on the local and regional scale (Appendix D). In the first case, I have explained the results in terms of a carbon allocation hypothesis, in which faster growing tree species allocate less carbon to the soil since the downward carbon flow is used for stem growth, whereas in the second case, I have suggested that when trees are growing faster in a forest stand, more carbon is being fixed by the ecosystem, thus more is also available, on average, to supply denitrification.

These seemingly contradictory explanations may be reconciled if one recognizes that above vs. below ground carbon allocation may vary from species to species within a stand. Such allocation should vary much less when averaged across all species within a stand, and thus when compared from stand to stand. An alternative hypothesis can be brought forward for this paradox: fast growing tree species need more nitrogen for their growth and compete more strongly with the soil microbes for nitrogen, leaving less substrate for denitrification, whereas in faster growing forest sites more nitrogen is available overall and thus associated with higher N$_2$O fluxes. This thesis does not contain observations of the key mechanisms for the hypothesis: 1) tree carbon export to soil varies from tree to tree (or stand to stand), and 2) that this variation correlates in the expected way with (a) N$_2$O flux on the back end, and (b) tree growth rates on the front end. However, current increased capabilities to measure specific microbial
activities, through meta-transcriptomic and proteomic analysis, shows great potential to address these shortcomings by mechanistically linking the microbial N$_2$O production — and whether it is driven by carbon limitation — to above ground tree species specific or forest growth. Direct sampling methods of root exudates and root nutrient uptake, through in-situ root isolation in a sterile soil-like medium, could be developed for clay-rich soils to determine how these change with species growth rate within and overall growth rate between stands. Lastly, more detailed root exclusion experiments (sampling different species within stand and stands with differing growth rates) will also help elucidate the specific influence of root on soil N$_2$O fluxes.
REFERENCES


Butterbach-Bahl, K., M. Kock, et al. (2004). "Temporal variations of fluxes of NO, NO\textsubscript{2}, N\textsubscript{2}O, CO\textsubscript{2}, and CH\textsubscript{4} in a tropical rain forest ecosystem." Global Biogeochemical Cycles 18(3): -.


Tomer, A. and B. H. Pugesek (2003). Guidelines for the implementation and publication of structural equation models. Structural equation modeling: Applications in


APPENDIX A

SPATIAL AND TEMPORAL VARIABILITY OF SOIL CO₂ AND N₂O FLUXES IN A CLAY-RICH SITE IN THE TAPAJOS NATIONAL FOREST, EAST-CENTRAL AMAZONIA, BRAZIL

Joost van Haren
Ruth Varner
Rainmundo Cosme de Oliveira Jr
Changshen Li
Steve Frolking
Michael Keller
Scott Saleska

To be submitted to Global Change Biology
Spatial and temporal variability of soil CO$_2$ and N$_2$O fluxes in a clay-rich east-central Amazonian forest.

Joost van Haren$^1$, Ruth Varner$^2$, Raimundo Cosme de Oliveira Jr$^3$, Changshen Li$^2$, Steve frolking$^2$, Michael Keller$^2$, and Scott Saleska$^4$

Draft to be submitted to the Global Change Biology

Author affiliation:

$^1$Dept. Soil, Water, and Environmental Science, University of Arizona, Tucson, AZ, USA

$^2$University of New Hampshire, Durham, NH, USA

$^3$EMBRAPA Amazônia Oriental, Santarém, Pará, Brazil

$^4$Dept. Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ, USA

Corresponding author: Joost van Haren, Biosciences West, 1041 East Lowell Street, Tucson, AZ 85721, USA; jvanhare@email.arizona.edu, (520) 626-5838, Fax: (520) 621-9190.
Abstract

Controls on spatial and temporal variability of soil fluxes of key greenhouse gases are poorly understood. This is a particular problem in remote tropical locations where soil fluxes are thought to contribute a significant fraction to global budgets, but lack of infrastructure makes acquisition of flux data difficult. We measured soil CO$_2$ and N$_2$O fluxes at three spatial and temporal scales in a central-eastern Amazon forest: 1) high spatial coverage at a few sampling dates, 2) long-term intermediate spatial and temporal coverage, 3) and long-term high temporal resolution at eight locations. We collected the first two datasets using manual chambers, placed into the soil immediately before sampling, and the third with automated chambers that were permanently installed to facilitate long-term measurements. Long-term fluxes were positively correlated with seasonal precipitation. Automated chamber CO$_2$ and N$_2$O fluxes were, respectively, 36 and 70% lower than manual chambers during the same time interval. We attribute this reduction to the severance and subsequent exclusion of shallow fine roots during and after the installation of the chamber bases into the soil. Spatial variability of wet season fluxes across the forest was comparable to the long-term temporal variability in CO$_2$ (37, 38, and 29% CV) and N$_2$O (79, 74 and 72% CV for the spatial, temporal, and automated chamber datasets, respectively) fluxes. Process model simulations overestimated soil N$_2$O flux sensitivity to precipitation pulses and underestimated dry season N$_2$O fluxes, though these results need to be further tested through careful evaluation of all carbon cycling components. We recommend that
automated chamber bases not be inserted into the soil because this will excise and may exclude surface roots, which may be especially important in tropical forest flux dynamics.
Introduction

[1] Understanding the spatial and temporal variability of soil gas fluxes has been one of the holy grails of biogeochemistry [Groffman et al., 2009; Townsend et al., 2008; Vargas et al., 2010]. Though several important breakthroughs have been made over the past 20 years -more accurate and automated measurements [ButterbachBahl et al., 1997; Crill et al., 2000] and improved process based models such as Daycent [Del Grosso et al., 2005] and ForestDNDC-Tropica [Kiese et al., 2005]- large unexplained variance remains in most studies. A striking example of this is illustrated in two papers detailing the temporal variability of soil CO$_2$ fluxes in the EsecaFlor drydown experiments in the Caxiuana National Forest in eastern Amazonia [Metcalf et al., 2007; Sotta et al., 2006]. Although, both studies get the seasonal variability between dry and wet season, their explanations are quite different: one using soil temperature as the main driving factor [Sotta et al., 2006], the other root dynamics and soil moisture content [Metcalf et al., 2007]. Even more so than soil CO$_2$ fluxes, soil N$_2$O fluxes are poorly constrained, mainly due to the many factors that influence denitrification and the small spatial distances (meters) denitrification activity can vary [Groffman et al., 2009].

[2] The spatial and temporal variability in tropical forest are the result of a cascade of nutrient supply and changes in environmental conditions [Lodge et al., 1994]. Tropical forests generally have fast, open nutrient cycles and depending on the substrate age they are either considered nitrogen (air derived) or phosphorous, calcium, etc. (soil derived) limited [Chadwick et al., 1999; Vitousek and Sanford, 1986]. Most
primary growth forests in the Amazon basin are on old soils, which are limited in soil derived nutrients and are not nitrogen limited due to abundant legume species, which have the ability to fix nitrogen [Ometto et al., 2006]. Sugar and nitrate addition experiments in lowland tropical soils in Costa Rica [Nobre et al., 2001] and Rondonia [Garcia-Montiel et al., 2003] demonstrated that carbon addition most strongly increased the microbial activity and N-cycling. Plants are the main source of carbon in tropical ecosystems and although their carbon flow into the soil through litter and root inputs can be ~10 Mg-C ha\(^{-1}\) y\(^{-1}\), it appears that soil microorganisms (with a standing biomass of ~2 kg-C ha\(^{-1}\) [van Haren et al., 2010a]) are limited in their labile carbon supply.

[3] Spatial and temporal soil greenhouse gas flux variability is further enhanced because the gases are produced or consumed by a wide variety of organisms. Soil-to-atmosphere flux of CO\(_2\), the most important [IPCC, 2007] and best understood greenhouse gas, is the result of litter decomposition, root respiration, dead root decomposition, fungal respiration, soil faunal respiration, and soil microbial respiration. Separation of the different CO\(_2\) sources remains very difficult [Kuzyakov, 2006], especially since all flow of organic carbon from the atmosphere to the soil through the leaves. Field techniques, such as girdling [Hogberg et al., 2009] and root exclusion [Metcalf et al., 2007; Silver et al., 2005], are promising, create unnatural conditions which could interfere with component flux estimates. Nitrous oxide (N\(_2\)O) is the by-product of the N-cycle, which is mediated by bacteria and fungi [Hayatsu et al., 2008].
N$_2$O production can occur both under aerobic (nitrification, nitrifier denitrification, and aerobic denitrification by fungi) and anaerobic conditions (mainly denitrification). In the final step of denitrification N$_2$O is reduced to N$_2$. The ratio of N$_2$O-to-N$_2$ produced depends on labile carbon, nitrate, and oxygen availability and soil pH [Nommiik, 1956].

[4] Ultimately, the N$_2$O produced has to make it past the soil-atmosphere interface to constitute a flux, which means that it needs to diffuse from the production location to the atmosphere. Most tropical soils are well developed and gas transport is generally not limiting, except for short time periods after very large (>50mm) rainfall events and seasonally flooded areas. Drainage of tropical forest soils has been found so efficient that even on undulating terrain overland flow almost never occurs (Hodnett, 1997). Efficient water drainage, mainly through macropores, suggests efficient gas transport, which was found in tropical soils in La Selva [Nobre et al., 2001] and in the central Amazon basin [Davidson et al., 2004]. The seasonal (dry-wet season) variation in diffusive gas flux was considerable close to the soil surface, but minimal at soil depths below a few meters [Davidson et al., 2004].

[5] Since it is nearly impossible to capture all spatial and temporal variability at any site, process models have been developed to extend our theoretical and empirical knowledge beyond our sampling coverage. Li et al.[2000] developed a process based model (PnET-DNDC) for temperate forests, which combines above and below ground forest ecosystem dynamics (forest growth submodel, Photosynthesis-Evapotranspiration model, PnET) with soil biogeochemistry (the Denitrification-Decomposition submodel
model, DNDC). Their model structure is such that tree growth regulates N uptake, leaf litter production, and root dynamics; it allows for competition between trees and microbes for ammonia and nitrate. Increased tree growth can both positively and negatively impact N\textsubscript{2}O production by respectively increased supply of labile carbon or reduction of available nitrogen substrate. The only version of DNDC currently tested for tropical forests is the ForestDNDC-Tropica model [Kiese et al., 2005; Werner et al., 2007], which couples the DNDC model to the Lund-Potsdam-Jena Dynamic Global Vegetation model (LPJ-DGVM) model for the above ground characterization.

[6] In this paper we set out to determine the relative variability of soil gas fluxes at one single site within the Tapajos National Forest. Our specific goals were to determine: 1) whether spatial or temporal variability had a greater influence on the annual soil gas flux estimate, 2) to what extend soil gas fluxes measured with automated chambers captured the spatial flux variability, and 3) whether we could model the observed annual flux variability with a process based model (PnET-DNDC, [Li et al., 2000]).

**Methods**

[7] Our sample site is located ~67 km south of Santarém in the Tapajós National Forest (TNF) in the state of Pará, Brazil. Mean annual temperature in the region is 25.0\textdegree C and annual precipitation average is 1920mm with a pronounced dry season from July through December [Parrotta et al., 1995]. The forest vegetation are diverse with
~150 species ha\(^{-1}\) (diameter at breast height, DBH >10 cm) and 27 species per ha (DBH >35 cm). Soils at the km 67 site is texturally highly homogeneous and consist of clay-rich Oxisol (clay content >90% [Williams et al., 2002]). Eddy-covariance measurements have been operational at this site since 2002 [Saleska et al., 2003] and forest inventory measurements including tree diameter and dendrometer band measurements, litterfall, and coarse woody debris have been monitored since 1999 [Pyle et al., 2008; Rice et al., 2004].

[8] We collected soil gas fluxes using a three tiered system: 1) high spatial distribution with ~ 200 manual chamber locations within 20 ha of forest plots sampled during the wet season only, 2) 1 ha spatially distributed, monthly repeated manual soil gas measurements with up to 24 chambers, and 3) automated chamber measurements with eight chambers in ~0.5 ha (Figure 1). The manual chambers were installed and gas fluxes were measured according to Keller et al. [2005] and van Haren et al. [2010]. Briefly, the manual chambers consisted of a PVC base, which was installed ~2 cm into the soil, and a vented acrylic lid, which was placed on the base within 30 minutes of installation. Starting a minute after closure, every ten minutes we drew air from the chamber into a syringe; a full flux was taken within 1 hour. Syringes measured within 24 hours on a dual gas chromatograph (GC) system as described in van Haren et al. [van Haren et al., 2010]. CO\(_2\) measurements from the manual chambers from the temporal dataset were conducted with a vented chamber top and a Licor 6251 [Keller et al., 2005]. The automated chamber lids were closed 5 times a day by pneumatic cylinder
onto a ~43 by 43 cm square base, which was installed 10-15 cm into the soil. After closure, headspace gas was pulled through a Licor (6262) for CO$_2$ and a 1 ml inlet loop of a Shimadzu 14a GC (equipped with ECD at 320 °C) for N$_2$O at a rate of 1000 ml min$^{-1}$. CO$_2$ was measured every 12 seconds, but closure time was limited by the N$_2$O measurement which took ~3 min. Total closure times were 20 minutes, with a two hour delay between the eight chambers. This study increased both the spatial and temporal extent to which a single site has been studied. The three sampling methods were not all conducted at the same time, we compared fluxes from the three sampling schemes collected during times of the year with similar climatic conditions, i.e., wet or dry season. Forest growth rates were determined based on DBH measurements of all trees greater than 10 cm in approximately 20 ha plots. Approximately 1000 trees at km 67 were outfitted with dendrometry bands to measure their growth rates at subannual timescales [Rice et al., 2004]. Soil gas fluxes were predominantly measured with manual chambers [Davidson et al., 2004; Keller et al., 2005]. We used concurrent soil flux and dendrometry measurements at km 67 to compare monthly growth rates and Soil CO$_2$ and N$_2$O fluxes for a period over 3 years between 2001-2004.

[9] The N$_2$O flux data from all the different sampling strategies resulted in highly non-normal datasets, common in studies of soil N$_2$O fluxes [Keller et al., 1986; Matson et al., 1990]. All non-normal datasets were log transformed before analysis and back-transformed before reporting the results. We used the bootstrap method to create confidence intervals for the means differences of the various datasets. Since we only
had the large scale spatial data for the months of March though May, we sub-sampled the other datasets for this timeframe for direct comparison of means and mean variability. To gauge the relative magnitudes of spatial and temporal variability, we compared their full datasets. To test for spatial sample independence we used the geoR package in R to construct semi-variograms to determine the spatial co-variance of the spatial dataset.

[10] We used Structural Equation Modeling (SEM) to statistically determine the relative strength of the predictor variables on soil gas fluxes. SEM was developed to explain the overall covariation pattern of group of continuous variables. SEM requires a-priori development of one or several cause-and-effect models, which then can be tested with statistically robust measures, such as the Aikake Information Criterion (AIC). We used the polycor and SEM packages in R Fox [2006] to analyze our data. Our model was based on a wood ring-width model from Fritts [1976] and used the measured climatic and forest dynamics variables at our tower site [Rice et al., 2004] to predict both daily and monthly soil CO2 and N2O fluxes (Figure 1).

[11] We used both the ForestDNDC-Tropica and PnET-DNDC model to simulate the overall carbon and nitrogen dynamics of the Tapajos site. ForestDNDC-Tropica had been previously calibrated to tropical systems [Werner et al., 2007], but we had to calibrate the PnET-DNDC model to the Tapajos National Forest site by extracting site-based data for photosynthesis, respiration, and soil characterization from the literature (Table 1). We then modified the model parameters to optimize model outputs with the
existing Eddy-covariance tower, plot demography, phenology, soil moisture, and soil gas flux data from the site in the Tapajos National Forest. We ran the model for ten years with the same climate drivers (mean of the four years modeled) to ‘spin-up’ the model. After the ten years we ran the four years (2001-2004) in continuous fashion.

Results

[12] Both CO₂ and N₂O fluxes were spatially and temporally highly variable (Figures 2, 3, and 4). The spatial N₂O flux variability was twice the CO₂ flux variability (Figure 2, coefficient of variance was 70 and 37, respectively). For CO₂, the spatial and manual temporal datasets were characterized by a tight clustering around the mean (253±13 and 225±6 mg-C m⁻² h⁻¹ (wet season only, mean±95%CI), respectively) with a tail of high flux locations (‘hotspots’) reaching values 2.5 to 4 times the mean. The spatial dataset was constructed during three wet seasons (2005, 2006 and 2007, which were not statistically different) and locations close to trees (263±6 mg-C m⁻² h⁻¹) and far from trees (180±6 mg-C m⁻² h⁻¹, see also [van Haren et al., 2010]). Mean automated chamber CO₂ ranged from 86.4±1.7 to 178±3 mg-C m⁻² h⁻¹, with an overall mean annual flux of 122±2 mg-C m⁻² h⁻¹ (Figure 2 left hand graphs). Wet season automated chamber CO₂ fluxes (134±2 mg-C m⁻² h⁻¹) were ~40% lower than the manual chamber mean (Figure 3), whereas dry season fluxes were ~30% lower (107±3 to 191±5 mg-C m⁻² h⁻¹, respectively). Differences between automated chambers were larger in the wet season than the dry season, but remained consistent across the sampling period (Figure 4), for both CO₂ and N₂O.
[13] For N\textsubscript{2}O, spatial and manual temporal datasets were characterized by a long tail to high N\textsubscript{2}O fluxes (Figure 2). Their geometric mean N\textsubscript{2}O fluxes were 85.9±4.4 and 70.6±9.6 \, \mu g-N \, m^{-2} \, h^{-1} (mean±95%CI), respectively. Annual mean automated chamber N\textsubscript{2}O flux ranged from 4.6±0.3 to 47.6±3.3 \, \mu g-Nm^{-2}h^{-1}. During the 2004 wet season, when we had both temporal chamber measurements, the mean automated chamber N\textsubscript{2}O fluxes were a factor of 4 lower than the spatial and manual temporal sampling setup (16.6±0.3 vs. 70.6±9.6 \, \mu g-N \, m^{-2} \, h^{-1} for the automated and manual repeated chambers, respectively). In the dry season the manual chamber N\textsubscript{2}O flux was 22.8±1.2 \, \mu g-N \, m^{-2} \, h^{-1}, whereas the automated chamber flux 8.1±1.0 \, \mu g-N \, m^{-2} \, h^{-1}.

[14] Temporal variability was strongly tied to the precipitation seasonality, both for CO\textsubscript{2} and N\textsubscript{2}O (Figure 4). Linear regression analysis was used to demonstrate that annual and automated fluxes were best correlated with precipitation when averaged over 14 days for CO\textsubscript{2} and N\textsubscript{2}O (R\textsuperscript{2} values were respectively 0.5 and 0.1 for the manual, and 0.4 and 0.2 for the automated chambers). Monthly fluxes were also correlated with soil moisture content (WFPS) and tree growth rates quantified by dendrometry (Figure 5). Multiple linear regression (Table 1) and SEM modeling (Figure 6) with the monthly dataset suggest that tree growth rate is the strongest driver of soil N\textsubscript{2}O fluxes, whereas precipitation through air temperature is the main predictor for soil CO\textsubscript{2} fluxes. On a daily basis SEM modeling indicate that precipitation is the strongest driver of both CO\textsubscript{2} and N\textsubscript{2}O fluxes (Figure 7). Air temperature had a minor effect, while Gross Ecosystem Production (GEP, a proxy for photosynthesis) had the least influence.
[15] Our process based model runs for both the ForestDNDCtropica model and PnET-DNDC model were able to reproduce the annual flux variability (Figure 2b for N$_2$O fluxes, unrealistic soil respiration fluxes were not plotted). However, the models underestimate the soil moisture content and N$_2$O flux during the dry season, and the model is highly responsive to precipitation pulses. The PnET-DNDC model predicted the wood growth rates reasonably well and the daily growth rate correlated well with daily N$_2$O flux ($R^2 = 0.4$, data not shown).

**Discussion**

[16] We believe that the 36 and 70% lower fluxes (for CO$_2$ and N$_2$O respectively) measured with permanently installed automatic chambers relative to manual chambers was due to an underestimation of the fluxes by the former, most likely due to the cutting and exclusion of shallow soil roots. Insertion of chamber bases into forest soils has been previously observed to cause strong reductions in soil gas flux over time [Heinemeyer et al., 2011], or a strong increase on the short term [Matson et al., 1990]. These effects have been attributed to the cutting of roots, which leads to an increase in root derived labile carbon an increased flux in a couple of days to months [Matson et al., 1990; Silver et al., 2005], whereas over long periods of time it leads to a reduction of fluxes due to root exclusion [Heinemeyer et al., 2011]. Soil respiration partition experiments in the Tapajos National Forest found that litter, root, and heterotrophic microbial decomposition contributed approximately equally (~33%) to the overall flux at
this site (de Camargo, pers. comm.). Since we measured the fluxes within one hour after installation of the manual chamber bases and did not add leaf litter, we do not think that these measurements represent an overestimation even roots were cut by the temporary insertion (e.g., Matson et al. [1990]). Therefore we expect that the reduction in automated chamber flux was more plausible. Reduced soil CO$_2$ fluxes could be the result of either the absence or removal of litter, root exclusion, a combination of the two, or poor closure of the chamber lid. Our automated chamber design allowed for the influx of leaf litter and fine woody litter. On a weekly basis all the chambers were checked and larger sticks were removed to prevent complications with lid-closure. So we attribute the majority of the observed reduction in soil CO$_2$ flux to root severance. Several studies comparing manual and automated chambers [Breuer et al., 2000; Savage and Davidson, 2003], found little or no difference between the soil gas fluxes from automated and manual chambers. Both automated and manual chamber bases in these studies were left in the soil for the duration of the experiment after insertion into the soil to a similar depth, which suggests that both methods might have underestimated the actual flux. Our measured reduction in soil CO$_2$ flux of ~36% was larger than the expected root contribution (see above) and larger than trenching associated CO$_2$ flux reduction (24-35%) ~15 km south of our site [Silver et al., 2005]. This suggests that litter input was reduced as well, especially since it is unlikely that all the roots were severed even when the chamber base was installed to a depth of 5 cm.
The density of fine roots is highest in the top 5 cm, representing ~50% of the total root biomass in the soil [Silver et al., 2000].

[17] A chamber-induced reduction of fine roots in the shallow soil might also have caused the observed reduction of N₂O flux. Soil N₂O is the result of both nitrification and denitrification, most of which is produced by microbes in tropical soils. Denitrifiers are strict heterotrophs and need labile carbon to be active, which is why elevated denitrifier activity has been found in the root rhizosphere [Henry et al., 2008]. Exclusion of fine roots reduces addition of labile carbon to the soil through root exudation, which can be substantial 1-5% of all carbon fixed [Kuzyakov et al., 2007]. Based on tower GPP measurements [Pyle et al., 2008], this would amount to 0.3-1.5 Mg-C ha⁻¹ yr⁻¹, comparable to the total amount of carbon allocated to fine roots 1.0 Mg-C ha⁻¹ yr⁻¹ [Silver et al., 2005]. The labile carbon value is 200-1000 times the average standing biomass of the microbial community [van Haren et al., 2010]. If we presume that the chambers cut the shallow roots and cut off the labile carbon supply to denitrification, we infer that root derived carbon can be responsible for 75% of the N₂O produced during the wet season.

[18] We found that spatial CO₂ fluxes measured along the transects were 20% higher than manual repeated chamber measurements. Approximately the same difference was found for the CO₂ fluxes close to and far from large trees [van Haren et al., 2010], which suggests that our spatial sampling mean represents an overestimation of the actual soil respiration flux, due to an oversampling of soil locations close to large
trees. Based on our spatial GIS analysis of all tree along the transects [van Haren et al., 2010], assuming a sphere of influence [Zinke, 1962] around each tree that scaled with tree diameter—a tree of 1m in diameter had an influence sphere with radius of 5 m—, we calculated that the tree influence soil area is ~30% of the total soil surface. When we sum the area weighted tree influenced and far from tree means, we could reproduce the manual repeated mean CO₂ flux. Mean N₂O flux estimates were not affected since fluxes far from the trees were indistinguishable from the overall mean. That the N₂O fluxes were not affected suggests that a reduction in root density away from the trees not likely the main factor driving this difference. We found that bulk density was significantly higher away from the trees [van Haren et al., 2010], which suggests that gas diffusion could limit the CO₂ flux far from trees. Gas diffusion from deeper depth has been shown to contribute substantially to the overall CO₂ flux [Davidson et al., 2004], whereas soil N₂O fluxes originate from shallower depths (<25 cm) and thus less sensitive to changes in gas diffusivity. Alternatively, the higher bulk density could produce more anaerobic micro-sites close to the soil surface, and thus increase the denitrification potential.

[19] Through linear and multiple linear regression and SEM analysis, we found a strong correlation seasonally between soil CO₂ and N₂O fluxes and tree growth rates, which on a monthly basis was the strongest predictor of soil gas fluxes (Figure 6). In our simplified SEM model tree growth rate was the strongest factor directly influencing soil N₂O fluxes, then soil moisture (WFPS), and soil temperature was not significant. The
results were different for the daily dataset, using the automated chambers, where NEE was not strongly related to N$_2$O flux. In our monthly model, NEE was a poor predictor variable for tree growth (Figure 8). Ecosystem variables such as Net Ecosystem Exchange have to our knowledge never been considered in the testing of soil N$_2$O fluxes. Besides soil moisture content, which is obviously also very important at our site, most often soil N$_2$O fluxes have been correlated both with soil CO$_2$ [Garcia-Montiel and Binkley, 1998], litter deposition, and C-to-N ratios [Klemetsson et al., 2005], and mineralization rates [Matson et al., 1990]. These are all components that represent the link between mineralization and nitrification, a major source of N$_2$O fluxes in drier, sandier soils [Davidson et al., 2000]. Soils in our site are clay-rich and are more conducive to denitrification, especially during the wet season, similar to soils measured ~15 km to the south [Keller et al., 2005]. Soil CO$_2$ and N$_2$O fluxes were both affected by the seasonal changes in precipitation, but only were poorly correlated with moisture during the wet season, when most N$_2$O flux activity occurs. Litter deposition was mainly driven by a strong increase in litter-fall during the early dry season [Rice et al., 2004], and thus strongly anti-correlated with soil N$_2$O fluxes.

[20] The process models (PnET-DNDC and ForestDNDC-tropica) could reproduce the observed general annual variability in N$_2$O flux, but they appear to greatly overestimate the responsiveness of the soil community to precipitation events. Both models overestimated the root respiration and consequently soil CO$_2$ flux, which is not surprising for the tropical forest uncalibrated PnET-DNDC model, but the ForestDNDC-
Tropica model was calibrated to tropical forest. Adjustment of the respiration temperature dependence parameter \( Q_{10} \) did not change this imbalance. During calibration the PnET-DNDC created an instability in the program that a sudden increase in plant nitrogen uptake after 5 model years. This reduced soil nitrogen content and \( \text{N}_2\text{O} \) flux by a factor of five-to-ten, depending on the nitrogen deposition conditions. At this point we have not been able to resolve these issues and therefore admit that the preliminary modeling results need to be tested further. Our experience with interpreting the modeling results suggests that process based models need to be thoroughly tested to existing data, which comprise all components of the model. This implies that process models can only be applied to sites where ecosystem measurements are on hand in combination with soil gas fluxes.

[21] We made two key findings during our modeling efforts that validate our model use: 1) temporal model simulated fluxes were more sensitive to precipitation variability than the measured mean manual and automated fluxes and 2) both models under-predict the soil \( \text{N}_2\text{O} \) fluxes during the dry season. The former was due to our comparison between the model and the chamber mean, which smoothed out most of the within chamber variability. Model results were much better correlated with the within chamber variability, than the mean fluxes. We interpret this to imply that spatial variability in resource flow in the soil is not captured by the model, which in a sense only represents the temporal variability at one micro-site. Local variability can be very large as had been found, by both our spatial sampling design, but also from our automated
chambers. The latter result most likely is tied to the shallow soil parameterization (0.3 m), which excludes a deeper soil gas reservoir for diffusive gas fluxes. [Davidson et al., 2004] found that maximum N$_2$O production occurred at 0.3 m depth, whereas CO$_2$ production occurred meters deep in the soil. Gas diffusion from depth can moderate soil gas flux variability over time scales of days rather than weeks or months [van Haren et al., 2005], which means that slow upward diffusion soil gas during dryer periods keeps field fluxes at a higher level than the model predicts.

**Conclusion**

[22] Our comparison of three spatial and temporal soil gas flux datasets in one tropical forest ecosystem site demonstrates that trees have a large influence on soil gas fluxes. By combining soil gas flux measurements at three different spatial and temporal levels with two different methods we demonstrated that: 1) in tropical soils automated chamber have to reside on the surface of the soil and not cut even the litter layer. Although many studies have found that horizontal gas diffusion can lead to underestimation of the soil gas fluxes [Hutchinson and Rochette, 2003], current gas chromatographic techniques can measure a reproducible flux in ten minutes. In tropical forests, where wind is nearly absent in the understory, the underestimation of the soil gas flux through horizontal diffusion is likely to be negligible. 2) the spatial variability of soil gas fluxes is of the same order of magnitude as the temporal variability, even in a
seasonally dry tropical forest, and 3) although process models can reproduce observed data, only if the whole ecosystem is modeled properly, can we attempt to predict what future feedbacks in soil gas fluxes to climate change might be.
References


Heinemeyer, A., C. DiBene, A.R. Lloyd, D. Tortorella, R. Baxter, B. Huntley, A. Gelsomino, and P. Ineson, Soil respiration: implications of the plant-soil continuum and respiration chamber collar-insertion depth on measurement and modelling of


Williams, M., Y.E. Shimabukuro, D.A. Herbert, S.P. Lacruz, C. Renno, and E.B. Rastetter,

Table 1. Multiple regression and correlation coefficients for mean daily and monthly fluxes for CO$_2$ and N$_2$O. The CO$_2$ fluxes were also broken down by season.

<table>
<thead>
<tr>
<th></th>
<th>Precipitation</th>
<th>NEE</th>
<th>ST 30 cm</th>
<th>Intercept</th>
<th>$R^2$</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>All daily</td>
<td>7.5±0.6</td>
<td>2.8±0.6</td>
<td>-4.2±1.3</td>
<td>202±35</td>
<td>0.43</td>
<td>137,350</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Jan-Mar</td>
<td>0.13±0.03</td>
<td>ns</td>
<td>ns</td>
<td>0.6±0.2</td>
<td>0.51</td>
<td>72,138</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Apr-Jun</td>
<td>0.08±0.04*</td>
<td>ns</td>
<td>0.18±0.02</td>
<td>2.0±0.7</td>
<td>0.38</td>
<td>29,299</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Jul-Sep</td>
<td>0.19±0.03</td>
<td>0.11±0.04</td>
<td>-0.12±0.04</td>
<td>3.4±1.4</td>
<td>0.74</td>
<td>45,470</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Oct-Dec</td>
<td>0.13±0.03</td>
<td>0.07±0.03</td>
<td>ns</td>
<td>1.7±0.3</td>
<td>0.48</td>
<td>25,385</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Monthly</td>
<td>0.26±0.08</td>
<td>0.39±0.23</td>
<td>ns</td>
<td></td>
<td>0.56</td>
<td>14,333</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>N$_2$O</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>All</td>
<td>0.16±0.03</td>
<td>ns</td>
<td>ns</td>
<td>-2.0±0.3</td>
<td>0.36</td>
<td>60,216</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Monthly</td>
<td>0.20±0.10</td>
<td>0.88±0.27</td>
<td>-0.23±0.14</td>
<td>7.8±3.7</td>
<td>0.74</td>
<td>31,333</td>
<td>&lt;0.0001</td>
</tr>
</tbody>
</table>

*denotes precipitation summed over 10 not 14 days. *based on manual chamber measurements. Bold values denote $P<0.0001$, whereas regular txt values signify $P<0.05$. 
Figure captions.

Figure 1. Our sampling scheme at the km 67 eddy covariance site in the Tapajos National Forest, ~67 km south of Santarem, Para, Brazil. Forest inventory transects were located to capture forest dynamics in the area most influential to the eddy flux tower. Dots along the transects denote the spatial soil sampling locations. The temporal sampling locations are located close to the tower as indicated by the arrows.

Figure 2. Soil CO$_2$ (top) and N$_2$O (Bottom) flux distributions from the three chamber datasets. The temporal datasets (automated and manual were separated in dry (July through Oct) and wet season (February through May) part of the dataset, the transition months were not shown.

Figure 3. Seasonality of soil gas fluxes coincides with precipitation variability. Bottom graph contains the temporal variability of precipitation (grey bars) and measured (black dots) and modeled (red line) soil water content. The center graph contains N$_2$O fluxes from automated (blue line) and manual (black dots) chambers and modeling results (red line). The top graph CO$_2$ fluxes for the automated (blue line) and manual (black dots) chambers. For clarity the points have been connected by a line, which does not reflect a filling method.

Figure 4. Large spatial soil gas flux variability is apparent from individual automated chamber soil CO$_2$ (top) and N$_2$O (bottom) flux trends with time. Each color denotes a
different chamber. The colors in the two graphs do not necessarily correspond to the same chamber.

Figure 5. Regression plots of the monthly soil CO\(_2\) (top) and N\(_2\)O (bottom) fluxes and (from left to right) tree growth rate, soil temperature, precipitation, and soil moisture (%WFPS). The trend lines all (except for CO\(_2\) and soil temperature) were highly significant at \(P < 0.0001\). CO\(_2\) fluxes are bi-modally related to soil temperature, we therefore separated the data in dry (closed diamonds, July through October), transition (open squares, November through January and June) and wet season (closed triangles, February through May).

Figure 6. Structural equation modeling of monthly climate forest dynamics, and soil N\(_2\)O fluxes suggests that precipitation and tree growth are the strongest predictors for soil N\(_2\)O fluxes. Precipitation both directly and through air temperature are the most important driver for the daily CO\(_2\) variation. Arrow size and superscripts indicate the \(P\)-value of each regression or path. Also given for each path are the unstandardized coefficient—or slope—and standard error.

Figure 7. Structural equation modeling of monthly climate forest dynamics, and soil N\(_2\)O fluxes. Precipitation both directly and through air temperature are the most important driver for the daily CO\(_2\) variation. The significance of soil moisture on monthly N\(_2\)O flux becomes only marginally significant (\(P=0.06\)) when the path between soil temperature and N\(_2\)O flux is removed (not shown). Arrow size and superscripts indicate the \(P\)-value
of each regression or path. Also given for each path are the unstandardized coefficient
—or slope—and standard error.
Figure 1

- 1 ha plot
  - Sampled 2x month
  - 8 chamber locations
  - 2001-2004
  - manual chambers

- 19.75 ha of transects
  - homogeneous soil
  - sampled 10 times
  - April-June 2005-2007
  - manual chambers

- <1 ha area
  - 2004
  - auto chambers (8)
  - Sampled 4-6x a day

Northern extent TNF

- Belterra
- Santarem
- BR-163
Figure 3
Figure 4
Figure 5
Figure 6

- Precipitation
  - Light
    - Air T
    - Soil T
  - %WFPS
    - Tree GR
    - N₂O flux

Arrows and coefficients:
- 1.9 ± 0.7 (from Precipitation to %WFPS)
- -0.03 ± 0.001 (from %WFPS to Light)
- 0.02 ± 0.003 (from Air T to %WFPS)
- -0.12 ± 0.05 (from Air T to Soil T)
- 0.04 ± 0.01 (from Soil T to Tree GR)
- 0.03 ± 0.03 (from %WFPS to Tree GR)
- 0.04 ± 0.01 (from Tree GR to N₂O flux)
- 1.04 ± 0.28 (from Tree GR to N₂O flux)
- -0.18 ± 0.16 (from Soil T to N₂O flux)
Figure 7
APPENDIX B

DO PLANT SPECIES INFLUENCE SOIL CO$_2$ AND N$_2$O FLUXES IN A DIVERSE TROPICAL FOREST?

Joost van Haren
Cosme de Oliveira Jr
Natalia Restrepo-Coupe
Lucy Hutyra
Plinio de Camargo
Michael Keller
Scott Saleska

Do plant species influence soil CO$_2$ and N$_2$O fluxes in a diverse tropical forest?

Joost L. M. van Haren,$^{1,2}$ R. Cosme de Oliveira Jr.,$^3$ Natalia Restrepo-Coupe,$^2$ Lucy Hutny,$^2$ Plinio B. de Carvalho,$^4$ Michael Keller,$^5$ and Scott R. Saleska$^6$

Received 25 November 2009; revised 12 March 2010; accepted 26 March 2010; published 4 August 2010.

[1] To test whether plant species influence greenhouse gas production in diverse ecosystems, we measured wet season soil CO$_2$ and N$_2$O fluxes close to 300 large (>35 cm in diameter at breast height (DBH)) trees of 15 species at three clay-rich forest sites in central Amazonia. We found that soil CO$_2$ fluxes were 38% higher near large trees than at control sites >10 m away from any tree ($P < 0.0001$). After adjusting for large tree presence, a multiple linear regression of soil temperature, bulk density, and liana DBH explained 19% of remaining CO$_2$ flux variability. Soil N$_2$O fluxes adjacent to Caryocar villosum, Lecythis lucida, Schinopsis murrensis, and Manilkara huberi were 84%–196% greater than Eriosa uncinata and Vochysia maxima, both Vochysiaceae. Tree species identity was the most important explanatory factor for N$_2$O fluxes, accounting for more than twice the N$_2$O flux variability as all other factors combined. Two observations suggest a mechanism for this finding: (1) sugar addition increased N$_2$O fluxes near C. villosum twice as much ($P = 0.05$) as near Vochysiaceae and (2) species mean N$_2$O fluxes were strongly negatively correlated with tree growth rate ($P = 0.002$). These observations imply that through enhanced belowground carbon allocation liana and tree species can stimulate soil CO$_2$ and N$_2$O fluxes (by enhancing denitrification when carbon limits microbial metabolism).

Alternatively, low N$_2$O fluxes potentially result from strong competition of tree species with microbes for nutrients. Species-specific patterns in CO$_2$ and N$_2$O fluxes demonstrate that plant species can influence soil biogeochemical processes in a diverse tropical forest.


1. Introduction

[3] Species' influence on ecosystem functions remains a fundamental, outstanding question in ecosystem ecology (Lavorel, 1994). In forests, knowledge of tree species' influence on soil CO$_2$ and N$_2$O fluxes is important for scaling these fluxes from the chamber to the ecosystem level (Hall and Ainsworth, 2007) and predicting ecosystem feedbacks to climate change (Torsqvist et al., 2008). Climatically, CO$_2$ and N$_2$O are both potent greenhouse gases, and N$_2$O leads to stratospheric ozone destruction (Crutzen, 1970). Biologically, soil CO$_2$ is a useful measure of ecosystem decomposition rates and root productivity, while N$_2$O is an indicator of nitrogen cycling processes (Galloway et al., 2001).

[4] Soil CO$_2$ and N$_2$O fluxes are spatially and temporally highly variable, especially in the tropics, where soil gas fluxes are generally high (Breuer et al., 2000; Batnich and Schlesinger, 1992) and measurements are scant (Breuer et al., 2000; Luyssaert et al., 2007; Werner et al., 2007). Development and application of automated chamber techniques have revealed that temporal N$_2$O flux variability in tropical forests is strongly coupled to precipitation changes (Kiese et al., 2003). Spatially distributed, manual chamber measurements have been used to show that soil N$_2$O fluxes are higher and more variable on clay-rich than sandy soils. In contrast, soil CO$_2$ fluxes are much less affected by soil texture (Breuer et al., 2000; Keller et al., 2005; Osaki et al., 2007) but can be related to soil moisture and temperature (Suits et al., 2004), fine root content (Schneidermann et al., 2003; Meschede et al., 2007), and forest structure (Kasugai et al., 2009).

[5] Studies in temperate ecosystems and plantations (Butterbach-Bahl et al., 2002; Binkley and Menge, 2005) have demonstrated that plant species can influence soil N$_2$O production and that proximity to tree individuals (Butterbach-Bahl et al., 2002) and community assembly can be critically

---

$^1$Department of Soil, Water, and Environmental Science, University of Arizona, Tucson, Arizona, USA.
$^2$Departments of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona, USA.
$^3$EMBRAPA Amazônia Oriental, Sanaúncim, Pará, Brazil.
$^4$Department of Geography and Environment, Boston University, Boston, Massachusetts, USA.
$^5$Universidade de São Paulo, CENA, Piracicaba, São Paulo, Brazil.
$^6$University of New Hampshire, Durham, New Hampshire, USA.

Copyright 2009 by the American Geophysical Union.
0148-0227/10/2009G001251
important [Valkama et al., 2006]. The only species-level study on samples collected in tropical regions [Menzies et al., 2003] linked CO$_2$ and N$_2$O production from soil cores to tree species located in low-diversity plantations. We set out to test whether tree species influence soil CO$_2$ and N$_2$O fluxes in high-diversity primary tropical forest. We measured soil gas fluxes, soil temperature (T$_{soil}$), bulk density (BD), soil moisture (SM), tree mass growth rate (MGR), and all stems >1 cm within a 3 m radius from the flux location close to CEN5 and 25 cm away from (±10 m) large individuals of 15 species. All measurements were conducted in three sites within a single primary forest in central Amazonia. To maximize potential soil flux variability, all measurements were conducted during the late wet season (April, May, and early June) of 2006 and 2007, since moisture becomes a limiting factor to greenhouse gas fluxes in the dry season [Davidson et al., 2004; Kellner et al., 2005].

2. Methods

2.1. Site Description

[5] We selected three primary forest sites (termed km 67, km 72, and km 83), all located within 2 km of each other in the Tapajos National Forest (TNF) south of Santarem, Pará, Brazil. Mean annual temperature in the region is 25.0°C, and annual precipitation average is 1920 mm with a pronounced dry season from July through December [Parrott et al., 1999]. The forest vegetation is diverse with ~150 species ha$^{-1}$ (diameter at breast height, DBH > 10 cm) and 27 species per hectare (DBH > 35 cm). Soils at the km 67 and km 72 sites are texturally highly homogeneous and consist of clay-rich Oxisol (clay content > 90%, see Table 1). At km 83, soils are texturally more variable [Silver et al., 2000], and we only selected sites with sand content <20%.

2.2. Sampling Design and Analyses

[6] Fifteen tree species (Table 2) were selected based on abundance (% basal area) and canopy status (upper canopy or emergent species only) from within 20 ha of transects established between 1999 and 2003 [Kyle et al., 2009]. Our species selection included one pioneer species (Schefflera morototoni) and four legume species (Caesalpinia multicarpa, Chamaecrista xinguensis, Pseudorpisodium paucotoxos, and Sclerolobium chrysothele), which can potentially form a symbiosis with N-fixing rhizobia bacteria. Of the species selected, most abundant at km 67 were Erythrina umbrosa, Manilkara huberi, Couratari stellata, and C. xinguensis with over 100 individuals >35 cm and 21%, 19%, 17%, and 11% of all basal area, respectively. Least abundant were Caryocar villosum, Vochysia maxima, Bertholletia excelsa, and S. morototoni with 12, 11, 9, and 12 individuals, respectively, and ~2% of basal area each. All individuals selected were >35 cm DBH, which because of their age and size were expected to exert more influence on soil processes. We determined mass growth rate (MGR) from biomass increment over time, calculated from periodic DBH measurements using the allometry of Chambers et al. [2001]. We identified by common name and measured the DBH and

### Table 1. Site Characteristics and Fluxes

<table>
<thead>
<tr>
<th>Site</th>
<th>Coordinates or Year</th>
<th>%Sand</th>
<th>MGR$^a$ (mg C m$^{-2}$ d$^{-1}$)</th>
<th>CN$^a$</th>
<th>ST (°C)</th>
<th>BD (g cm$^{-3}$)</th>
<th>%WFPS</th>
<th>pH</th>
<th>CO$_2$ (mg C m$^{-2}$ d$^{-1}$)</th>
<th>N$_2$O (μg N m$^{-2}$ d$^{-1}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>km 67</td>
<td>2.880S 125.014W</td>
<td>5.4 (1.3)</td>
<td>20.6 (0.8)</td>
<td>12.4 (0.6)</td>
<td>24.9 (0.04)</td>
<td>6.72 (0.04)</td>
<td>54.7 (0.5)</td>
<td>3.67 (0.04)</td>
<td>219 (7)</td>
<td>85.82 (5.45)</td>
</tr>
<tr>
<td>km 67</td>
<td>2.880S 125.014W</td>
<td>24.7 (0.03)</td>
<td>6.72 (0.03)</td>
<td>52.5 (0.05)</td>
<td>NA</td>
<td>244 (6)</td>
<td>3.67 (0.04)</td>
<td>212 (11)</td>
<td>82.15 (3.2)</td>
<td></td>
</tr>
<tr>
<td>km 67</td>
<td>2.880S 125.014W</td>
<td>25.3 (0.02)</td>
<td>7.62 (0.06)</td>
<td>59.4 (5.9)</td>
<td>NA</td>
<td>245 (11)</td>
<td>3.67 (0.04)</td>
<td>212 (5)</td>
<td>84.65 (4.2)</td>
<td></td>
</tr>
<tr>
<td>km 72</td>
<td>2.915S 125.048W</td>
<td>1.0 (0.4)</td>
<td>13.9 (0.5)</td>
<td>13.1 (0.2)</td>
<td>25.0 (0.06)</td>
<td>7.67 (0.06)</td>
<td>57.0 (1.5)</td>
<td>3.45 (0.06)</td>
<td>243 (11)</td>
<td>44.46 (2.4)</td>
</tr>
<tr>
<td>km 83</td>
<td>3.025S 125.038W</td>
<td>17.5 (0.8)</td>
<td>18.3 (1.1)</td>
<td>13.3</td>
<td>25.7 (0.06)</td>
<td>8.61 (0.02)</td>
<td>69.1 (1.2)</td>
<td>3.59 (0.06)</td>
<td>226 (11)</td>
<td>85.71 (6.3)</td>
</tr>
</tbody>
</table>

$^a$Value denote mean (SE); bold values are greater than change in radius (r = 0.08).

### Table 2. Species Used for Flux Measurements

<table>
<thead>
<tr>
<th>Family</th>
<th>Genus</th>
<th>Species</th>
<th>Authority</th>
<th>Common Name</th>
</tr>
</thead>
<tbody>
<tr>
<td>Anacardiaceae</td>
<td>Anacardium</td>
<td>locustae</td>
<td>(Dac.)</td>
<td>Jacaranda</td>
</tr>
<tr>
<td>Anacardiaceae</td>
<td>Schellinbera</td>
<td>morototoni</td>
<td>(Aubl.) Maguire</td>
<td>Morototoni</td>
</tr>
<tr>
<td>Caryaaceae</td>
<td>Carya</td>
<td>villosa</td>
<td>(Aubl.) Pers.</td>
<td>Quale</td>
</tr>
<tr>
<td>Fabaceae</td>
<td>Fabaceae</td>
<td>caesalpinia</td>
<td>(Dac.) H.S. Irwin &amp; Barneby</td>
<td>Coratia de norte</td>
</tr>
<tr>
<td>Fagaceae</td>
<td>Fagaceae</td>
<td>planofoe</td>
<td>(Dac.)</td>
<td>Copal</td>
</tr>
<tr>
<td>Fagaceae</td>
<td>Fagaceae</td>
<td>typhina</td>
<td>(Dac.)</td>
<td>Copal</td>
</tr>
<tr>
<td>Ficusaceae</td>
<td>Ficus</td>
<td>minor</td>
<td>(Buch.)</td>
<td>Carianda de Pará</td>
</tr>
<tr>
<td>Lecythidaceae</td>
<td>Lecythidaceae</td>
<td>velutina</td>
<td>(Dac.)</td>
<td>Jacaranda</td>
</tr>
<tr>
<td>Lecythidaceae</td>
<td>Lecythidaceae</td>
<td>verticilata</td>
<td>(Bert.)</td>
<td>Andringa</td>
</tr>
<tr>
<td>Malpighiaceae</td>
<td>Malpighiaceae</td>
<td>guajumus</td>
<td>(Dac.)</td>
<td>Macheles</td>
</tr>
<tr>
<td>Sapindaceae</td>
<td>Sapindaceae</td>
<td>huberi</td>
<td>(Dac.)</td>
<td>Açaia</td>
</tr>
<tr>
<td>Sachaeanthaceae</td>
<td>Sachaeanthaceae</td>
<td>reticulata</td>
<td>(Eng.)</td>
<td>Açaia</td>
</tr>
<tr>
<td>Vochysiaceae</td>
<td>Vochysiaceae</td>
<td>umbrosa</td>
<td>Wams.</td>
<td>Açaia</td>
</tr>
<tr>
<td>Ypomoeaceae</td>
<td>Ypomoeaceae</td>
<td>ulicina</td>
<td>Dac.</td>
<td>Açaia</td>
</tr>
</tbody>
</table>

*Tree species were initially identified in 1999 along the km 67 transect by Nelson A. Reis from the Museu Emilia Freire in Belém, Brazil, where voucher specimens are stored in the museum collection. During our field campaign Nelson de Souza Carvalho 2004 EMBRAPA office in Belém, Brazil, conducted all the tree identifications. All tree species are also described in the Treat of the Tapajós [Parrott et al., 1995].
distance from the chamber of all stems greater than 1 cm within a radius of 3 m from the flux location. Liana stems were measured at 1.3 m from the first rooting location and not identified by species. Immediately after taking the fluxes, we measured \( T_{\text{soil}} \) and pH in situ in four locations within the chamber area with handheld probes (Omega PH222 meter with PHAT-222 temperature probe, accurate at ±0.1°C, and PHE-2350 mäg pH probe, accurate at 0.02 with a two-point, pH 4 and 7, calibration before and after every batch of measurements). We collected soil samples (0–3 cm depth) for bulk density (BD) and soil moisture (SM) analyses by inserting soil rings (diameter = 5 cm; height = 3 cm) into the soil surface. The rings were immediately weighed and dried at 105°C for at least 24 h. BD was determined by dividing the soil dry weight by the ring volume and percent water filtered through a 0.45-µm filter (SM was calculated from BD and SM according to Linn and Duran [1984]). After drying, we selected 45 soil samples from three species with differing N-O fluxes, removed, and weighed root and litter fractions before measuring C and N content on a Carlo Erba Elemental Analyzer at CENA, Piracicaba, São Paulo, Brazil. We measured microbial biomass using the fumigation and extraction method on freshly sampled soils collected close to 6 randomly selected Caryocar villosum, Eriodictyon cruciatum, and Vochysia maxima trees.

2.3. Soil Gas Fluxes

[1] To measure soil gas fluxes, we installed ~30 cm diameter chamber bases ~2 cm into the soil and within 1 h (to minimize root decomposition effects) drew four 20 ml, B&D plastic syringes at 10 min intervals. Within 36 h, we analyzed all syringes for CO₂ and N₂O on a Shimadzu gas chromatograph with 2 ml injection loop, Porapak Q column (1.8 × 4.5; P₃-carrier head pressure at 40 psi, and column temperature at 60°C), and electron capture detector at 300°C. Gas fluxes were determined using linear regression and converted to weight area⁻¹ time⁻¹ using air temperature and chamber volume. In 2007, we measured soil gas fluxes immediately before and ~30 min after glucose addition to the soil (2.5 g m⁻² in 20 L of water) to assess the instantaneous response of the existing soil community to sugar addition [Nobre et al., 2001; Garcés-Montiel et al., 2005].

2.4. Data Analyses

[4] Measured parameters were tested for normality and log-transformed when appropriate; geometric mean and standard error (SE) values were reported in Tables 2 and 4. Statistical analyses were conducted in JMP (SAS, USA). For both the whole data set and for each species separately, we tested different regression models using liana DBH and sum DBH within 3 m of the flux location, \( T_{\text{soil}} \), BD, and % WFPS in JMP. In each case, the alpha level was 0.05, and the best regression model was chosen based on the Akaike Information Criterion (AIC) value. The final model was chosen based on the lowest AIC value. AIC was calculated as

\[
\text{AIC} = -2 \ln L + 2k
\]

where \( L \) is the maximum likelihood of the model, and \( k \) is the number of parameters in the model. The Akaike weight (\( w_i \)) of each model was calculated as

\[
w_i = \frac{\exp(-\Delta_i)}{\sum_j \exp(-\Delta_j)}
\]

where \( \Delta_i \) is the difference between the AIC of model i and the model with the lowest AIC. The model with the highest Akaike weight is the best model. The final model was selected based on both the lowest AIC value and the highest Akaike weight. To determine the relative importance of each potential predictor variable to obtain their relative importance according to the study of Johnson and Omland (2004).

2.5. Impact of Species Composition on Ecosystem-Scale Fluxes

[1] In order to estimate how changes in tree species composition might influence the overall forest fluxes and greenhouse gas balance, we used a simple model to scale ecosystem fluxes. We calculated annual fluxes based on dry season fluxes from Keller et al. [2005], who measured soil CO₂ and N₂O fluxes at one of our sites in 2001 and 2002, and a 6 month wet season [Ferreira et al., 1996]. We assumed no flux difference between species in the dry season. Then, we added the wet season effect of tree species’ influence depending on the species identity and the size of the trees. To accomplish this, we entered tree location and size of all trees >35 cm into ArcGIS (USRI, USA) to obtain the circle of influence and overlap [e.g., Zinke, 1962] for each tree species. We assumed that circle of influence was scaled linearly with DBH and calculated the influence area per species for when the circle of influence at DBH of 100 cm was between 1.5 and 15 m. Areas of all combinations of flux influence (control, tree species, and tree species overlap where fluxes were averaged) were multiplied by the appropriate flux and weighted by the total area. Population changes were mimicked by increasing or reducing the proportional area of influence of the species with high or low fluxes.

3. Results

3.1. Overall Flux and Soil Parameter Differences

[1] CO₂ and N₂O fluxes ranged from 39 to 767 mg-C m⁻² h⁻¹ and 5 to 595 µg-N m⁻² h⁻¹, respectively, values comparable to other tropical forests during the wet season [Brener et al., 2000; Odaishi et al., 2007]. Abnormally high N₂O fluxes (800 mg-C m⁻² h⁻¹, n = 33) could have been the result of termitic activity [Odaishi et al., 2007], though association of high CO₂ with high N₂O and CH₄ fluxes, gases also emitted by termitic activity, was not consistent. We measured fluxes both in 2006 and 2007 at km 67, and except for %WFPS, all variables were nearly identical between years (Table 1). Our three forest sites had very similar mean CO₂ fluxes, but the N₂O flux at km 72 was ~50% lower than at both other sites (Table 1). We found no difference in mean CO₂ flux among the selected tree species (Figure 1). \( T_{\text{soil}} \), BD, liana DBH, and % WFPS explained respectively 46%, 8%, 8%, and 5% of the observed variability. Interaction between the liana DBH, \( T_{\text{soil}} \), and BD increased the explained variability to 24%. Tree species differences explained 16% of all N₂O flux variance, twice the variance explained by %WFPS (both \( P < 0.0001 \)), with some interactive effects between the different variables: \( AIC_{\text{species}} = -230, AIC_{\text{species+species}} = -265, \) and \( AIC_{\text{species+species+species}} = -255.5 \).

3.2. Flux and Soil Parameter Differences With Species Grouped by Day

[1] We found strong variability in the day-to-day mean fluxes, \( T_{\text{soil}} \), BD, %WFPS, CO₂, and N₂O fluxes (\( P < 0.15, 0.72, 0.13, 0.38, 0.15, \) and 0.24, all \( P < 0.0001 \)). This prompted us to reanalyze all data grouped by day. Species differences remained (Figure 1), with only a strong reduction in \( P \) value with \( T_{\text{soil}} \). With all sites combined, CO₂ fluxes close to large trees (2455 mg-C m⁻² h⁻¹, mean ± SD) were 38% larger than mean flux away from large trees (control,
Figure 1. (a) Tree mass growth rate (MGR), (b) soil pH, (c) bulk density (BD), (d) %WFPS, (e) CO₂ flux, and (f) N₂O flux in relation to tree species at three clay-rich sites in the TNF. All values were corrected for mean differences between sampling days. Horizontal continuous and dashed lines denote overall mean (n = 338) and 95% confidence interval (CI), respectively, while black diamonds and error bars denote species means ±95% CI. Legume (L) species are denoted with shading, and species means significantly greater and smaller at α = 0.01 are denoted with + or −, respectively. AL, Astronium lecointei (n = 17); BL, Borreria reticulata (n = 11); CG, Carapa guianensis (n = 28); CM, Coigue fimbriata (n = 7); CS, Couratari stellaris (n = 32); CV, Carya ovata (n = 23); CX, Chamaecrista xinguaensis (n = 13); EU, Eriopsis uncinita (n = 29); LL, Lecythis horrida (n = 33); MH, Manilkara huberi (n = 35); PP, Psidium guajava (n = 23); PR, Pouteria reticulata (n = 18); SC, Schirolechium chrysophyllum (n = 23); SM, Schefuella havanensis (n = 7); and VM, Voxtysia maxima (n = 17). Asterisk denotes control taken >10 m from any tree >35 cm (n = 33).
Figure 2. Soil CO₂ fluxes versus (a) $T_{	ext{soil}}$, (b) BD, (c) liana DBH, and (d) their multiple regression combination. The multiple regression explains ~23% of CO₂ flux variability. BD includes information on soil moisture (%WFPS) and total organic content (COC in the top 0–3 cm of the soil), since BD explains ~55% and 45% of variability in %WFPS and TOC, respectively.

Figure 1e, 177.4 mg-C m⁻² h⁻¹, $P < 0.0001$. Mean BD (0.83 ± 0.04 g cm⁻³, Figure 1e) and %WFPS (68 ± 3, Figure 1d) of the control samples were 15% and 24% greater, respectively, than the species mean ($P = 0.02$ and 0.01, respectively). $T_{	ext{soil}}$, BD, %WFPS, and liana DBH remained the strongest predictors for CO₂ fluxes explaining 14%, 11%, 8%, and 6% of CO₂ variability, respectively (Figure 2). Multiple regression between $T_{	ext{soil}}$, BD, and liana DBH explained 23% of total variance, 18% after adjusting for the difference between close and away from large trees.

Mean N₂O fluxes close to C. villasna (104.7 µg-N m⁻² h⁻¹, Figure 1e) were 111% and 147% larger than close to E. uncinatum and F. maxima (49.6 µg-N m⁻² h⁻¹ and 42.3 µg-N m⁻² h⁻¹, respectively, $P < 0.005$ Tukey-Kramer HSD test). While L. lurideae, the most productive species, explained 12% greater than E. uncinatum, the L. lurideae, S. morototoni, and M. huberi explained 116%, 106%, and 104% greater than F. maxima, respectively, at $P < 0.05$. Tree species still explained more N₂O flux variance (12%) than any other variable, with %WFPS, MGR, and pH explaining ~4%, 2%, and 3%, respectively. When taking the population averages, only regressions with %WFPS and tree MGR were significant ($P < 0.005$ and 0.002, respectively), explaining 43% and 52% of species-to-species variability (Figure 3).

Figure 3. Species-specific soil N₂O fluxes versus (a) %WFPS, (b) mass growth rate (MGR), and (c) their combination. Vochoyniaceae N₂O fluxes ($r^2 = 0.97$, large dashed line) versus 0.39 (solid line) for all species (dashed line for species defined separately, more positive trend with %WFPS than most other species (small dashed line, $r^2 = 0.70$). The negative trend between N₂O flux and MGR is significant, especially when S. morototoni, a pioneer species, is excluded ($r^2 = 0.48$ and 0.69, respectively). Note that because of the negative correlation with N₂O, the sign of the MGR and %WFPS coefficients is the opposite of what is expected.
### Table 3. Slope Direction, Summed Akaike Weight, Adjusted Correlation Coefficients, and P Values for the Multiple Linear Regressions by Species for By-DO Correlated CO₂ Fluxes and N₂O Fluxes Also After By-Species Correction

<table>
<thead>
<tr>
<th>Species</th>
<th>Linear DBH*</th>
<th>Sum DBH*</th>
<th>ST</th>
<th>BD</th>
<th>%WFPS</th>
<th>R² adj</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>All</td>
<td>10.99</td>
<td>11.00</td>
<td>0.98</td>
<td>0.52</td>
<td>0.52</td>
<td>0.52</td>
<td>0.23</td>
</tr>
<tr>
<td>A. leucotricha</td>
<td>10.67</td>
<td>0.62</td>
<td>0.25</td>
<td>0.08</td>
<td>0.08</td>
<td>0.08</td>
<td>0.21</td>
</tr>
<tr>
<td>B. stenolepis</td>
<td>10.87</td>
<td>0.87</td>
<td>0.78</td>
<td>0.09</td>
<td>0.09</td>
<td>0.09</td>
<td>0.48</td>
</tr>
<tr>
<td>C. gigantea</td>
<td>10.64</td>
<td>10.86</td>
<td>11.00</td>
<td>0.51</td>
<td>0.51</td>
<td>0.51</td>
<td>0.51</td>
</tr>
<tr>
<td>C. arborescens</td>
<td>10.87</td>
<td>0.87</td>
<td>0.78</td>
<td>0.09</td>
<td>0.09</td>
<td>0.09</td>
<td>0.48</td>
</tr>
<tr>
<td>C. villisoma</td>
<td>10.87</td>
<td>0.87</td>
<td>0.78</td>
<td>0.09</td>
<td>0.09</td>
<td>0.09</td>
<td>0.48</td>
</tr>
<tr>
<td>L. laricina</td>
<td>10.87</td>
<td>0.87</td>
<td>0.78</td>
<td>0.09</td>
<td>0.09</td>
<td>0.09</td>
<td>0.48</td>
</tr>
<tr>
<td>M. kahni</td>
<td>10.87</td>
<td>0.87</td>
<td>0.78</td>
<td>0.09</td>
<td>0.09</td>
<td>0.09</td>
<td>0.48</td>
</tr>
<tr>
<td>P. polystachya</td>
<td>10.87</td>
<td>0.87</td>
<td>0.78</td>
<td>0.09</td>
<td>0.09</td>
<td>0.09</td>
<td>0.48</td>
</tr>
<tr>
<td>S. montana</td>
<td>10.87</td>
<td>0.87</td>
<td>0.78</td>
<td>0.09</td>
<td>0.09</td>
<td>0.09</td>
<td>0.48</td>
</tr>
<tr>
<td>V. maximus</td>
<td>10.87</td>
<td>0.87</td>
<td>0.78</td>
<td>0.09</td>
<td>0.09</td>
<td>0.09</td>
<td>0.48</td>
</tr>
</tbody>
</table>

*Linear DBH and sum DBH represent the sum of DBH measurements within a 5 m radius of the soil flux location of all trees and species × 1 cm DBH, respectively. Species not mentioned did not have a correlation between any independent and dependent variable P value less than 0.10.

### 3.3. Species-Specific Regressions

[i] The multiple regression analysis conducted separately for each species, had much higher explanatory value than the overall regression (Table 3). The mean species R² adj was higher than the R² adj for the regression with all samples (CO₂: 0.36 versus 0.23, z = 1.8, P = 0.04; N₂O: 0.39 versus 0.04, z = 9.3, P = 0). This even was true for N₂O after assuming R² adj = 0 for not reported species (0.17 versus 0.04, z = 2.5, P = 0.007). We found that for 6 species, CO₂ fluxes correlated positively with liana DBH (Table 3). We further found 5, 3, 2, and 3 correlations between CO₂ flux and T_total (total DBH < 3 m), BD, and %WFPS, respectively. Correlations between CO₂ flux and both liana DBH and T_total were consistently positive, whereas correlations with total biomass and %WFPS were not. Species-specific N₂O flux multiple linear regression analyses were almost all strongly positively correlated with %WFPS. Other consistent correlations were found for BD (3 times negative) and liana DBH (twice positive). Correlations with total DBH (3) and T_total (2) were not consistent.

### 3.4. Soil Measurements Near Species With Districting N₂O Fluxes

[i] We focused further analyses on the three species with the largest and most consistent N₂O flux differences. C. villisoma, E. uncinitum, and V. maximus (Table 4). Soil analyses revealed no difference for CN ratio, [NO₃⁻], and microbial biomass, only a weakly significant difference in either litter or fine root content between soil samples collected close to C. villisoma and E. uncinitum or V. maximus individuals, respectively. Sugar additions resulted in an immediate response in CO₂ and N₂O fluxes, which were contrasted correlated with the initial N₂O flux (P = 1.71, R² = 0.82, and P < 0.001). CO₂ fluxes increased by 25% to 70%, whereas N₂O fluxes increased by 46% close to C. villisoma and by ~33% close to E. uncinitum and V. maximus individuals (Table 4).

### 3.5. Impact of Tree Species on Ecosystem Fluxes

[i] In general, tree species-related N₂O flux differences, and the soil CO₂ flux difference between species and control, were both substantial relative to the overall greenhouse gas budget of this forest. On an equal global warming potential basis (N₂O ~ 296 times CO₂), annual species N₂O flux differences represent approximately half of the net flux of CO₂ from the ecosystem and 10% to 20% of the carbon annually stored as net growth [Pyle et al., 2008].

[i] Our simple model of the spatial distribution of trees influenced ecosystem fluxes indicated that the overall forest CO₂ flux was 15% greater than the control mean CO₂.

### Table 4. Soil Measurements Near Species With Districting N₂O Fluxes

<table>
<thead>
<tr>
<th>Species</th>
<th>N₂O (µg N m⁻² h⁻¹)</th>
<th>CN Ratio</th>
<th>Litter (Og)</th>
<th>Fine Root (g)</th>
<th>[NO₃⁻] (µg l⁻¹)</th>
<th>MB-C (µg C g⁻¹)</th>
<th>xN₂O Increase</th>
<th>CO₂/N₂O (1000)</th>
</tr>
</thead>
<tbody>
<tr>
<td>C. villisoma</td>
<td>123(7)</td>
<td>14(30.2)</td>
<td>3(60.7)</td>
<td>3.2(12.9)</td>
<td>1.23(2.9)</td>
<td>3.4(10.9)</td>
<td>2.2(7.2)</td>
<td>7(22.3)</td>
</tr>
<tr>
<td>E. uncinitum</td>
<td>4(7)</td>
<td>13.7(14.3)</td>
<td>2.0(13.3)</td>
<td>1.4(10.8)</td>
<td>1.2(13.4)</td>
<td>7(10.9)</td>
<td>2.2(7.2)</td>
<td>7(22.3)</td>
</tr>
<tr>
<td>V. maximus</td>
<td>35(6)</td>
<td>14.5(28.3)</td>
<td>3.4(10.9)</td>
<td>1.3(12.9)</td>
<td>1.4(11.4)</td>
<td>7(10.9)</td>
<td>2.2(7.2)</td>
<td>7(22.3)</td>
</tr>
</tbody>
</table>

*From left to right: mean (SE), N₂O flux, soil CN ratio, litter, fine root content, [NO₃⁻], microbial biomass (MB-C), N₂O flux increase after sugar addition, and CO₂/N₂O ratio.

*CN ratio, litter, and fine root content were determined on the same samples that were used to measure BD and %WFPS. Bold values are significantly different from italic values (Tukey-Kramer α = 0.05 for all except N₂O and CO₂/N₂O, where α = 0.0002 and 0.0005, respectively). Subscripts and superscripts in parentheses denote the same group at both positive and negative values.
flux when the tree circle of influence was >7.5 m. This is a realistic size for the range of tree influence since maximum tree root extent measured, when trenches were dug for a large-scale drought experiment, nearby in the TNF were 30–34 m for three tree species (M. huberi, L. berdiana, and E. encrustatum) (O. Nepstad, personal communication). The modeled ecosystem-scale N\textsubscript{2}O flux did not change appreciably when the root circle of influence was increased, due to the presence of tree species with both higher and lower than average fluxes. The ecosystem-scale N\textsubscript{2}O flux, as estimated from the spatially explicit distribution of trees, is comparable to the N\textsubscript{2}O control flux measurements (>10 m away from any large tree >35 cm DBH). Only a large shift (20%–25%) in ecosystem composition from tree species with either higher to lower fluxes (or vice versa) would have an appreciable effect (>15% of the overall flux) on ecosystem N\textsubscript{2}O fluxes.

4. Discussion

4.1. Potential Causes for CO\textsubscript{2} Flux Differences

[7] We found no tree species effect on CO\textsubscript{2} fluxes, but the effect of presence or absence of large trees was presumably a consequence of litter or root density. Lower fine root density or litter content [Schneidermann et al., 2003; Metcalfe et al., 2007] have been demonstrated to correspond with reduced CO\textsubscript{2} fluxes. Similar to Soto et al. [2004], we found no correlation between total forest biomass (measured within 3 m of the flux location) and soil CO\textsubscript{2} flux, as found in various ecosystems by Karzmuza et al. [2009], who included a range of measurement radii around their flux measurements. However, we do not expect that the difference in sampling radii would affect the correlation in our case, since Karzmuza et al. [2009] found a >30% explanatory power for total DBH when measuring only trees >10 cm within 3 m of each flux location (their Figure 4).

[8] Beyond the effect of presence or absence of nearby trees and the expected effect of soil climate (positive effect of temperature, Park and Clark [1996], we observed, for the first time, a distinct effect of liana DBH on soil respiration. As far as we know, this paper is the first to demonstrate a positive correlation between liana DBH and soil CO\textsubscript{2} efflux. Two aspects of liana physiology make this relationship highly plausible: (1) liana leaves are located in the upper canopy with high light exposure and have high water use efficiency [Domazgus et al., 2007]; and (2) lianas have to invest less carbon into structural biomass [Pata, 1983] and, compared to trees, should have more carbon to invest below ground. The negative relationship between BD and soil CO\textsubscript{2} efflux, which could be a consequence of either lower soil density in high BD soils, or a BD correlation with pore space, which controls the soil gas transport flux to the atmosphere. Since we did not observe strong relationships between root density and soil CO\textsubscript{2} efflux, we presume that reduced gas transport is the main mechanism for BD influence on soil CO\textsubscript{2} fluxes.

4.2. Potential Causes for N\textsubscript{2}O Flux Differences

[9] Perhaps our most interesting finding is the high importance of tree species composition, even in a diverse primary forest, on the magnitude of N\textsubscript{2}O fluxes. In fact, our data confirm that tree species identity was the single most important factor in explaining flux variability, more than twice as important as soil water. For example, when considering the species mean N\textsubscript{2}O fluxes, the two Vochysiaceae species and control samples appear to define a more sensitive trend of N\textsubscript{2}O flux to soil moisture relative to all other species (dashed line, Figure 3a). There are many hypotheses immediately suggested by the literature, but on close examination, many of these seem implausible. In tropical forests, for example, differences in soil N\textsubscript{2}O fluxes have been linked to litter decomposition rates [Kiers et al., 2003], soil CN ratios [Kiers and Butterbach-Bahl, 2002], pH [Menyantho et al., 2003], %WFPS [Davidson et al., 2004], and texture [Keller et al., 2005]. By selecting only clay-rich soils, we did not address the influence of soil texture on N\textsubscript{2}O fluxes. Species-specific litter decomposition did not appear to influence soil mineralization rates since CO\textsubscript{2} fluxes were species independent. This is consistent with litter mixing experiments in diverse tropical forests, which render litter decomposition rates relatively independent of location and species [Schöner-Lorenzen et al., 2007]. Neither site-averaged (Table 1) nor species-specific (Table 3) soil N\textsubscript{2}O fluxes and CN ratios supported the correlation between annual N\textsubscript{2}O fluxes and site-averaged CN ratios, as observed by Kiers and Butterbach-Bahl [2002]. Soil CN ratio has been tied to ecosystem mineralization and nitrification rates, but its relation to soil nitrification rates is less clear. Since all our sampling was conducted in clay-rich soils during the wet season, in a forest where foliar and soil N\textsubscript{15}N values are suggestive of denitrification [Williams et al., 2002], we expect denitrification to be the more dominant process causing spatial N\textsubscript{2}O flux variability. After correcting for the dry measured, we found a small negative correlation between pH and soil N\textsubscript{2}O fluxes. However, species or site mean N\textsubscript{2}O fluxes correlated neither negatively nor positively with soil pH as observed by Menyanto et al. [2003]. A negative correlation between pH and N\textsubscript{2}O fluxes is expected in acidic soils based on the inhibitory effect of low pH on the N\textsubscript{2}O reductase enzyme [Nömni, 1996].

4.2.1. N\textsubscript{2}O Fluxes and Legume Species

[10] Surprisingly, N\textsubscript{2}O fluxes close to trees from the Leguminosaeae family (denoted by dotted areas in Figure 1) were not particularly high. Even the biomass of small legume trees, which are more likely to be nodulated [de Paris et al., 1998; Sprent, 2003, 2005], within 3 m of the chamber location did not appear to influence the soil N\textsubscript{2}O fluxes (data not shown). Legumes have been found to restore N dynamics in secondary forests [Davidson et al., 2007], and soil N\textsubscript{2}O fluxes have been found to increase in areas where invasive legume trees dominated wet tropical forests in Hawaii [Hall and Arner, 2007]. In the TNF, high N\textsubscript{15}N values and high foliar N content [Williams et al., 2002] suggest that legumes add little N to the ecosystem. Lack of nodulation found in the field as implied by high N\textsubscript{15}N values of leaf nitrogen could account for the lower than expected N\textsubscript{2}O fluxes for the legume species.

4.2.2. Potential Plant Drivers of Soil Biogeochemistry

[11] Given that most measured soil physical and chemical parameters explain less of the soil N\textsubscript{2}O flux variability than plant species, we propose that plant-soil interactions drive soil N\textsubscript{2}O fluxes in complex forests. Plants are the main source of carbon, a major source of nitrogen to soils, and potentially compete with soil microorganisms for nutrients [Schimel and Bennett, 2004]. We can envision two mechanisms that could explain a direct relationship between tree species and soil N\textsubscript{2}O fluxes: (1) tree species could alter soil N\textsubscript{2}O fluxes...
through the quality and quantity of C added to the soil (e.g., labile carbon would be expected to stimulate denitrification [e.g., Scaglia et al., 1985]) and/or (2) trees could compete with soil microorganisms for nutrients and thereby directly or indirectly affect denitrification. Though not mutually exclusive, we will treat these two processes as such in the following discussion.

[3] In tropical forest soils, soil microorganisms are generally carbon, rather than nitrogen, limited [Nobre et al. 2001; Garcia-Montiel et al., 2005]. High \( \frac{N}{N} \) values of total soil pools and leaves in the TFN [Williams et al., 2002] are consistent with sufficient available N and thus substrate limitation of N loss through denitrification [Grossman et al., 2006]. Our sugar additions confirmed that the soils in the TFN were C limited but that carbon limitation could be quite variable. We interpret the tree response after sugar addition of soils close to C. villosaum and lack of microbial biomass to imply that these soils are more prone to denitrification. Furthermore, since more denitrification produces CO\(_2\) and N\(_2\)O at a 1:1 ratio [Barford and Bremner, 1975] and decomposition processes produce these gases at a 5000:1 ratio [Garcia-Montiel et al., 2002], areas with high denitrification activity could produce high N\(_2\)O fluxes without changing the CO\(_2\) flux. Keller et al. [2005] measured high CO\(_2\)/N\(_2\)O ratios (~30,000) in sandy Ultisols but low ratios (~1500) in clay-rich Oxisols during the wet season under conditions conducive to denitrification. The low CO\(_2\)/N\(_2\)O ratios and greater reduction in CO\(_2\)/N\(_2\)O ratio after sugar addition closer to C. villosaum are consistent with stimulated denitrification closer to C. villosaum.

[4] Alternatively, the flux difference among tree species could be the result of more-specific competition with soil bacteria for nutrients, as suggested by Schimel and Bennett [2004]. Trees derive most of their nutrients from the surrounding soil, except for some N uptake through fixation and by precipitation interception. The soil nutrient demand of trees depends on their overall nutrient demand, which is tied to their overall growth rate [Irigoyen and Ayres, 1992], their efficiency in precipitation interception, the amount of photosynthesis per unit of nutrient, and their efficiency in retaining nutrients during senescence. Although we did not demonstrate such competition effects in the TFN, a recent study in the Brazilian Cerrado by Kocovksy et al. [2007] found that N and P resorption was much greater in Caryocar brasiliense, same genus as C. villosaum, than in Qualea parviflora, which belongs to the Vochysiaceae family. As a result, litter N concentrations were similar and presumably C. brasiliense had more N and P stored in woody tissue to provide for the next leaf flush. The authors interpreted these results to imply that Q. parviflora had to derive more of its nutrients from the soil. In the TFN, we observed shallow root mats more commonly around E. uncinatum and V. maxima than C. villosaum, suggesting that the Vochysiaceae invest more biomass in shallow soil nutrient uptake. This was only partially confirmed by the root content in our shallow soil samples (Table 4). Furthermore, we found that tree species’ mean N\(_2\)O fluxes were negatively correlated with Mg, especially when a pioneer species (S maritima) was excluded (clashed line, Figure 2b). Fast growing trees generally have higher nutrient demands [Irigoyen and Ayres, 1992] and therefore need to compete more strongly for nutrients with the microbial pool, which could lead to reduced N\(_2\)O fluxes. Pioneer species are expected to fall off this trend, since pioneers are adapted to low nutrient conditions. Legume species normally would be expected to follow this trend, though lack of nodulation in the TFN would negate this.

5. Conclusion

[4] We found that tree species and lianas can influence soil biogeochemistry, especially N cycling in complex tropical forests. However, we are troubled by the overall low explanatory power of any of the measured variables for either soil CO\(_2\) or N\(_2\)O fluxes. This suggests that in tropical forests under the wet conditions of the rainy season, we still do not understand well what processes drive spatial flux variability. This is consistent with our poor understanding of denitrification activity across the globe [Grossman et al., 2006]. Furthermore, soil C\(_\text{TN}\) ratios, the standard way to incorporate plant species into biogeochemical models, cannot explain the large N\(_2\)O flux differences observed between control and TFN. We propose that species-dependent resource acquisition strategies, such as those underlying species-specific growth rates and nutrient demand functions, are more important for soil biogeochemistry than previously appreciated. Incorporation of plant species traits may be important for successful N\(_2\)O production models. The influence of lianas on both CO\(_2\) and N\(_2\)O fluxes is evidence of their importance on carbon balance of tropical ecosystems and their importance as belowground resource competitors. Since lianas are expected to increase in abundance in tropical systems with increased fragmentation and climate change [Phillips et al., 2002], this might represent a further negative climate change feedback combined with the reduction in tree growth rates observed by van der Heijden et al. [2009].

Acknowledgments. The authors thank the USDA Savannah eSignature Program for logistic support and Francisco Alves Freitas, Chacon Perera, Jackson da Silva, Marcello de Souza Feitosa, Felipe Saraiva, and Nilson de Souza Cardoso, for their invaluable help in the field. Virginia Rich and Eric Davidson for their comments on an earlier version of the paper. The research was conducted with U.S. Forest Service funding through grants to M.K. and a NSF-PIRE Fellowship to J.S.M.

References

Bertzky, B., and O. V. Mutanga (2005), Tree species effects on nutrient implications for global change, NTD Science Series 4, pp. 358.


103
APPENDIX C

TROPICAL TREE SPECIES EFFECTS ON SOIL PROPERTIES AND GREENHOUSE GAS FLUXES IN MONOCULTURE AND DIVERSE FORESTS

Joost van Haren

Raimundo Cosme de Oliveira Jr

Michael Keller

Scott Saleska

Advanced draft to be submitted to Plant and Soil
Tropical tree species effects on soil properties and greenhouse gas fluxes in monoculture and diverse forests.

Joost van Haren\textsuperscript{1,4}, Raimundo Cosme de Oliveira Jr.\textsuperscript{2}, Michael Keller\textsuperscript{3}, and Scott Saleska\textsuperscript{1,4}

Advanced draft to be submitted to Biotropica or Plant and Soil

Author affiliation:

\textsuperscript{1}Dept. Soil, Water, and Environmental Science, University of Arizona, Tucson, AZ, USA

\textsuperscript{2}EMBRAPA Amazônia Oriental, Santarém, Pará, Brazil

\textsuperscript{3}University of New Hampshire, Durham, NH, USA

\textsuperscript{4}Dept. Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ, USA

Corresponding author: Joost van Haren, Biosciences West, 1041 East Lowell Street, Tucson, AZ 85721, USA; \texttt{jvanhare@email.arizona.edu}, (520) 626-5838, Fax: (520) 621-9190.
Abstract

Tropical plantations are considered a viable option to recover abandoned agricultural lands, but the implications of management practices (especially tree species composition) for non-CO$_2$ greenhouse gas budgets on such plantations have been little studied. We investigated plant species influence on soil pH, bulk density (BD), moisture content (%WFPS), and soil greenhouse gas fluxes in three forest sites and monoculture plantation plots. We selected the same nine species in the undisturbed forest sites and plantation, all on clay-rich soils of the Belterra formation, in east-central Amazônia, Brazil, and conducted all measurements during the wet season in 2006, 2007, and 2009.

Semi-variogram analysis of all measured variables revealed that >90% of sample variance was explained by a nugget effect and that samples were spatially independent when more than 5m apart. We found that soil BD was 18% higher, and soil CH$_4$, CO$_2$ and N$_2$O fluxes and %WFPS were 78, 12, 62, and 18% lower on the plantation than in the forest. Soil pH was similar at both forest types. The lowest N$_2$O fluxes overall were measured on legume plots within the plantation. Soil BD, %WFPS, temperature, and CH$_4$ and CO$_2$ fluxes varied strongly (P<0.01) with tree species plots in the plantation, but not in the forest. N$_2$O fluxes differed among species in both locations, but species rank order in the forest was unlike that found in the plantation. Structural equation modeling suggests that BD and temperature are the strongest indicators of soil CO$_2$ fluxes in both the plantation and the forest, whereas species and %WFPS are the best
predictors of soil N$_2$O fluxes in the forest and species and temperature on the plantation.

Our study indicates that 1) that species influence soil processes, but such species effects are different between monoculture plantations and forests, and 2) high tree growth and low CH$_4$, CO$_2$ and N$_2$O soil emissions imply a reduced climate forcing effect from plantations, especially when planted with fast-growing legume species on abandoned farmland.

Keywords: plantation, Amazon, legume, carbon dioxide, nitrous oxide, tree growth

Highlights

> We measured tree species’ soil gas fluxes on a monoculture plantation and several forest sites. > Monoculture soil properties differed with tree species and legume plots had high growth rates and low N$_2$O fluxes. > In both locations, tree species influenced soil N$_2$O fluxes, though their rank-order was very different. > Tree growth was the most important quality for the overall climate change feedback. > Tropical plantations on abandoned farmland have a negative feedback on climate change.
1. Introduction

Tree plantations, currently covering more than 60 million ha globally and expanding rapidly in south-east Asia and south America (FAO, 2010), provide an important mechanism to recover abandoned agricultural and pasture lands in the tropics. Depending on the species selected, tropical tree plantations can provide multiple services such as pulpwood, hardwood, fruits, medicinal oils, and carbon sequestration (Silver et al., 2000). Though their expansion potentially will conflict with the need for food security in the tropics (DeFries and Rosenzweig, 2010), inclusion of native fruit trees and agroforestry options have the potential to achieve both goals of climate change mitigation and food security.

The impact of tree plantations on carbon budgets is large when monoculture or mixed plantations are planted on abandoned pasture or cropland (Montagnini and Nair, 2004). However few have investigated the methane (CH\(_4\)) and nitrous oxide (N\(_2\)O) budgets of plantation forests (Palm et al., 2002; Akimoto et al., 2005; Ishizuka et al., 2005; Arai et al., 2008). CH\(_4\) and N\(_2\)O have global warming potentials 23 and 296 times that of CO\(_2\) (IPCC, 2007) and N\(_2\)O has become the main cause for ozone destruction in the stratosphere (Ravishankara et al., 2009). Recently, mixed plantations have been promoted (Scherer-Lorenzen et al., 2005) since they sequester more carbon than monocultures and addition of N-fixing tree species does greatly increase the diameter growth rates of the non-fixing species (Piotto, 2008). In an overall greenhouse gas
balance, this positive growth enhancement could be offset by increased N\textsubscript{2}O fluxes from plantations including N-fixing species (Arai et al., 2008; Hergoualc'h et al., 2008).

The influence of tree species on soil processes has long been known (Binkley and Menyailo, 2005), but like the role of species in ecosystems (Lawton, 1994) remained difficult to quantify in diverse forests (e.g., Powers et al. (2004)). Researchers have argued that to avoid inherent soil variability we have to use monoculture plantations (common gardens) to determine tree species effects on soil nutrient and greenhouse gas production (Binkley and Menyailo, 2005; Brechet et al., 2009). Binkley and Menyailo (2005) also warn for the potential pitfalls of monocultures and that they are not a realistic rendering of nature and that the trees are consistently young. Mostly in monoculture (Montagnini and Sancho, 1990; Valverde-Barrantes, 2007; Brechet et al., 2009), but recently also in mixed species experiments (Piotto et al., 2004; Nichols et al., 2006; Niklaus et al., 2006; Murphy et al., 2008), studies have found that plant species can influence soil properties and processes. Mixed species experiments of litter decomposition (Hattenschwiler et al., 2005), nutrient cycling (Jacob et al., 2009), and above ground biomass growth (Piotto, 2008) have found that species effects are not additive and that species specific effects disappear in mixed cultures (Murphy et al. 2008). This begs the question: how realistic are monoculture derived plant species effects on soil properties and processes with respect to diverse forest settings?
In this paper, we compare tree species on a monoculture plantation and in a diverse forest with regard to associated soil physical characteristics and greenhouse gas fluxes. The goals were 1) to estimate the overall greenhouse gas impact of monoculture plots on a plantation vs. natural forest sites, 2) to determine tree species influence soil properties and gas fluxes on a native species, monoculture plantation, 3) to determine whether plantations carry predictive capability for tree species influence in a diverse forest, and 4) to determine whether climate and vegetation drivers had different effects on soil processes on the plantation vs. forest. We measured fluxes only in the wet season since many studies have found that dry season fluxes, and thus potential species differences, are greatly reduced compared to wet season fluxes (Breuer et al., 2000; Kiese et al., 2003; Butterbach-Bahl et al., 2004; Davidson et al., 2004; Keller et al., 2005; Werner et al., 2006; Metcalfe et al., 2007; Sotta et al., 2007; Werner et al., 2007a; Werner et al., 2007b; Murphy et al., 2008; Sotta et al., 2008; Brechet et al., 2009)

2. Methods and site description

2.1 Site description and species selection

We measured soil gas fluxes in three clay-rich, primary forest sites and one plantation site in and just north of the Tapajós National Forest (TNF) south of Santarém, Pará, Brazil (see Fig 1. and Table 1). Mean annual temperature in the region is 25.0°C and annual precipitation average is 1920mm with a pronounced dry season from July
through December (Parrotta et al., 1995). In the forest, vegetation dynamics transects were established in 1999 (Rice et al., 2004) and 2001 (Pyle et al., 2008). All trees >35 cm Diameter at Breast Height (DBH, at 1.3 m) were measured annually since 2005. The forest vegetation is diverse with 114 species in 20 ha (DBH >35 cm). Soils at the forest and plantation sites are texturally homogeneous and consist of clay-rich Oxisol (clay content >85%, Table 1; (Williams et al., 2002; van Haren et al., 2010)). Most abundant tree species are Carapa guianensis, Chamaecrista xinguensis, Couratari stellata, Erisma uncinatum, Lecythis lurida, Manilkara huberi, and Sclerolobium chrysophyllum, though their local abundance varies within the forest. In the forest, we previously selected 15 upper canopy or emergent species (Table 2), with legumes and shade-tolerant functional groups both represented (van Haren et al., 2010). Nine of the forest species were also represented in the plantation, where we measured soil gas fluxes on plots of ten different species.

The Empresa Brasileira de Pesquisa Agropecuaria (EMBRAPA) plantation in Belterra (Fig. 1) was established in 1978 on abandoned pasture farmland, which previously had been a rubber plantation (Russell, 1942). Species were planted in monoculture in variable size plots (0.01 to 0.5 ha) on very clay-rich soil (Table 1.). After establishment, the EMBRAPA plantation has been maintained throughout and kept relatively free of understory trees. Canopy development was dependent on the tree sun tolerance and ability to do well in plantation settings. Especially shade intolerant species such as Betholletia excelsa, C. guianensis, Copaifera multijuga, and L. lurida plots contain nicely
developed trees with dense canopies and therefore a clean understory. In contrast, *Astronium lecontei* and *M. huberi* plots are very open and thus allowed for more ingrowth. The understory and large litter was removed from all plots one to two days prior to the flux measurements. Based on forest abundance, plot clearing and stand density, we selected 9 species out of the 15 forest species and we added one legume species (*Hymenolobium excelsum*). We only were able to replicate plots for *B. excelsa*, *H. excelsum*, and *Vochysia maxima*, for which we measured three, two, and two separate plots, respectively. To determine whether individual samples were independent at the plot scale we applied semi-variogram analysis.

### 2.2 Flux and supporting measurements

All measurements have been described in detail in van Haren *et al.* (2010). We measured AT (air temperature) and ST (soil temperature) with handheld temperature probes (accurate at ±0.2 °C) and collected soil samples (0-3cm depth) for BD (bulk density) and SM (soil moisture) analyses in aluminum soil rings (diameter = 5 cm; height = 3 cm), which were weighed on the collection day and dried at 105 °C for at least 24 hrs. Percent water filled pore space (%WFPS) was calculated from BD and SM according to Linn and Doran (1984). We used a rugged gel-filled electrode (Omega PHE-2385) and Omega PHH222 pH/mV meter to measure soil pH in-situ (0-5cm depth and a mean of four locations within the gas flux ring). The electrode was calibrated every 8 samples to pH 4 and 7 buffers in the field and daily to pH 4, 7, and 10 in the lab.
In the forest, we measured soil gas fluxes within 0.5 to 3m from the stems of large (>35cm) randomly selected stems of each species. At each plot on the plantation, we placed chambers for flux measurements >5m from the edge of the plot, at random distances from the trees. All flux measurements were conducted during the late wet season, April, May, and early June of 2006, 2007, and 2009. We installed chamber bases ~ 2 cm into the soil and within one hour (to minimize root decomposition effects, e.g., (Matson et al., 1990; Varner et al., 2003)) drew four 20 ml B&D® plastic syringes at 10 minute intervals. Within 36 hrs, we analyzed all syringes for CO₂ and N₂O on a Shimadzu gas chromatograph with a 2 ml injection loop, Porapak Q column (1/8”x4’, P5-carrier headpressure at 40 PSI, and column T at 60 °C), and ECD detector at 300°C. Gas fluxes were determined using linear regression of the four measurements and converted to weight area⁻¹ time⁻¹ with the air temperature and chamber volume.

We measured the diameter at breast height (1.3m, DBH) of all trees within each plantation plot and within a 3m radius of the flux location in the forest sites. Tree growth rates in the forest were taken from the DBH measurements that have been conducted annually since 2005. Due to the relatively close spacing of the trees on the plantation, we did not use tree growth rates, but whole plot basal area (BA) as a proxy for vegetation growth, since all trees were planted at the same time as similar size seedlings. Biomass was calculated from the DBH measurements and wood density values according to Chave et al. (2005).
2.3 Statistical analyses

Measured parameters were tested for normality and log-transformed when appropriate and back-transformed before reporting. We used ANOVA in JMP (SAS) to compare all measured parameters with the Tukey-Kramer HSD procedure. We used the geoR package in R to construct semi-variograms for each of the soil parameters and gas fluxes to determine the range where samples would be considered spatially dependent. Linear, multiple, and stepwise regression procedures were applied to determine correlations between biological and soil parameters and gas fluxes. In all analyses, species were considered the treatment or fixed effects (Bennington and Thayne, 1994), all other parameters as random effects. The best fit model in MLR analysis was determined using the Akaike Information Criterium (AIC). The stepwise procedure in JMP was used to calculate the root mean square error of all possible models. Then we calculated the Akaike weight (w) of each model and the weight of each predictor variable using the equations in box 2 of Johnson and Omland (2004).

We conducted Structural Equation Modeling (SEM) with the SEM package in R (Fox, 2006) to assess the strength of the different predictor variables on the dependent variables. We developed simple models of the influence of the tree species on soil parameters and gas fluxes and then compared the different models for consistency of strength of predictor variables and the overall model fit. We used the cor package in R to calculate the covariance matrix with the pearson method using the cov command.
Multiple model comparative statistics, generated by the SEM package, are reported in the figures.

3. Results

3.1 Plantation vs forest overall

On average soil CH\textsubscript{4}, CO\textsubscript{2} and N\textsubscript{2}O fluxes and %WFPS were respectively 78, 12, 62, and 8\% lower on the plantation relative to the clay-rich forest sites (Tables 1). ST and BD on the plantation were respectively 2 and 18\% higher than the clay-rich forest sites. Soil pH was indistinguishable on plantation and forest clay sites. The biomass was highly variable on the plantation (ranging from \(\sim\)50-300 MgC ha\textsuperscript{-1}), though the mean was comparable to the forest sites (175\(\pm\)27 vs. 200\(\pm\)10 MgC ha\textsuperscript{-1} Table 3). Mean annual growth ranged from 1.5 to 10.1 MgC ha\textsuperscript{-1} y\textsuperscript{-1} on the plantation; higher than the forest site with mean growth rates of \(\sim\)3.9 MgC ha\textsuperscript{-1} y\textsuperscript{-1}.

3.2 Tree species differences

Semi-variogram analysis did not indicate any spatial dependency for most of the parameters and soil gas fluxes at the plot level (~2 m, Figure 3). Soil temperature (not shown), BD and WFPS did show some spatial dependency up to 20-30 m, though the nugget effect is very large for all, which suggests that most of the variance occurs within very small distances. We therefore treated all samples within a plot as independent
samples. For replicated plots we found that aboveground biomass (BA and LAI), soil properties and gas fluxes were nearly identical separate plots of *B. excelsa, V. maxima, and H. excelsum*, only ST was respectively 1.0, 0.7, and 0.9 °C lower on one of the plots. On the plantation, tree species explained a larger part of ST, pH, BD, %WFPS, CO₂ and N₂O flux variance than at forest sites (Table 3 and 4). We found that on the plantation mean soil CO₂ flux measured within *C. guinensis* plots was 75, 128, and 78% greater than in *C. multijuga, L. lurida, and V. maxima* plots, respectively (Table 3 and Figure 2). Extraordinarily high CO₂ fluxes on the *C. guianensis* plot were the result of a very thick (2-5cm) litter layer. When we removed the litter layer, the CO₂ flux was reduced by ~35% from 310±34 to 202±21 mg-C m⁻² h⁻¹ (P<0.01, n = 24), but the N₂O flux did not reduce significantly (69±15 to 60±16 μg-N m⁻² h⁻¹ P<0.35). Mean soil N₂O fluxes were 78 and 76% smaller within *S. chrysophyllum* plots than in *C. villosum* and *V. maxima* plots. Soil pH and BD were lowest in the *L. lurida* plot, which had also the smallest diameter trees and low soil CO₂ and N₂O fluxes. %WFPS in *V. maxima* plots was 21% greater than in *S. chrysophyllum* plots and soil temperature was 4.7 and 5.9% higher in the *A. lecontei* and *M. huberi* than in *V. maxima* plots. In the forest, we did not observe any species differences except for soil pH (higher close to *V. maxima* than *M. huberi* and *S. chrysophyllum*) and N₂O flux (*C. villosum* and *L. lurida higher* than *V. maxima*).

Legume plots in the plantation (*H. excelsum, C. multijuga, and S. chrysophyllum*) exhibited consistently lower CO₂ and N₂O fluxes, unlike the legume counterparts in the forest (*C. xinguensis, C. multijuga, P. psilostachya, and S. chrysophyllum*). Soil pH was
reduced close to legume trees or on legume plots (0.1 and 0.18 on plantation and in forest, respectively, p<0.01 for both, Table 5). On the plantation %WFPS and soil N$_2$O flux were lower on legume plots, while BD was greater. In contrast, %WFPS, BD, and N$_2$O fluxes close to forest legumes were indistinguishable from non-legume fluxes. All the above mentioned differences remained when only species means were compared (P<0.05, forest n=15 and plantation n=10).

We compared the relative ranking of species means only for soil N$_2$O fluxes and pH values, since only these had species level differences in both the forest and plantation (Table 3 and Figure 2). For N$_2$O fluxes we found a rank-order of *C. villosum*/ *C. multijuga*/ *L. lurida*/ *M. huberi*/ *B. excelsa*/ *A. lecontei*/ *C. guianensis*/ *S. chrysophyllum*/ *V. maxima* in the forest, and *C. guianensis*/ *C. villosum*/ *B. excelsa*/ *V. maxima*/ *A. lecontei*/ *M. huberi*/ *C. multijuga*/ *L. lurida*/ *S. chrysophyllum*, on the plantation. The pH rank orders were *V. maxima*/ *C. villosum*/ *A. lecontei*/ *C. guianensis*/ *L. lurida*/ *C. multijuga*/ *M. huberi*/ *S. chrysophyllum* in the forest, and *L. lurida*/ *C. villosum*/ *B. excelsa*/ *C. guianensis*/ *C. multijuga*/ *V. maxima*/ *M. huberi*/ *S. chrysophyllum* on the plantation.

3.3 Regression analysis and structural equation modeling

Tree species explained most of the soil N$_2$O flux variation at both the forest and plantation, while for CO$_2$ fluxes tree species were only important on the plantation (Table 4). Not surprisingly, best predictors for soil CO$_2$ fluxes were ST, BD, and %WFPS in
the forest and BD, species, pH and %SM on the plantation. Soil N$_2$O fluxes were, after species, best explained by %WFPS, pH, and BD in the forest and %SM, BD, and pH on the plantation (Table 4). In the forest, species mean N$_2$O fluxes were best explained by a Multiple Linear Regression (MRL) of tree GR, soil BD, T, and %WFPS ($R^2_{adj}=0.87$, $P=0.002$). Of the predictor variables the AIC order was GR, BD, %WFPS, and T, though the differences were small (1.00, 0.98, 0.96, and 0.95, respectively). Due to the lower within site differences in predictor variables and number of samples, plantation based MLR analyses were much less robust and did not improve regressions with CO$_2$ and N$_2$O fluxes. Overall and within the plantation site soil BD was by far the best predictor for soil CO$_2$ fluxes, with only a minor additive effect of soil T (Table 4).

Structural equation modeling revealed that the best models for both CO$_2$ fluxes were similar in the forest as well as the plantation, with BD and soil temperature as the strongest predictors (Figure 4a and c). The path between biomass and soil variables is much less strong in the plantation than in the forest (Figure 5a and c). The strongest path to explain N$_2$O fluxes was through soil temperature in the plantation, whereas in the forest this was through %WFPS. Inclusion of species through biomass or tree growth rate in the forest suggested that the strongest path was through BD for CO$_2$ and BD and %WFPS for N$_2$O (Figure 5b and d). Direct influence of the biomass or growth rate directly on soil gas fluxes only was suggested with biomass for CO$_2$ flux and growth rate for N$_2$O flux in the forest (Figure 5e and f).
4. Discussion

In this paper we set out to determine 1) the overall greenhouse gas impact of a plantation vs. natural forest, 2) tree species (in particular legume species) influence on soil properties and gas fluxes on a native species monoculture plantation, 3) whether plantations studies improve predictive capability for tree species influence in a diverse forest, and 4) whether climate and vegetation drivers had different effects on soil processes on the plantation vs. forest.

4.1 Overall comparison forest vs. plantation

Plantations replacing abandoned agricultural lands represent a viable option to offset some human carbon emissions (Silver et al., 2000; Montagnini and Nair, 2004; Russell et al., 2010). In our study the overall stored biomass on the plantation was similar to the forest, though the variability on the plantation was very large (Table 3). Soil gas fluxes measured in the forest sites were similar to fluxes measured previously during the wet season in the TNF (Keller et al., 2005; Davidson et al., 2008) and the plantation fluxes were similar to wet season fluxes reported from sandy forest sites in the TNF (Keller et al., 2005; Silver et al., 2005). Our plantation N₂O fluxes were 3 to 4 times larger than those measured on agriculture sites older than 4 years just outside the TNF (Wick et al., 2005). Soil N₂O fluxes from the agricultural, plantation, and primary forest sites in and around the TNF follow a similar increasing trend with age compared
to secondary forests in Paragominas, Brazil (Davidson et al., 2007). This suggests that plantation monocultures have a positive effect on soil nitrogen cycling like secondary forests, in agreement with tree-based systems and secondary forests in Peru (Palm et al., 2002). Consequently, with increasing plantation age soil N$_2$O fluxes are expected to increase and the net benefit with respect to greenhouse gas balance decreases. The scenario is consistent with the analysis of Silver et al. (2000) who found that medium age rotations (40-80 years, when tree carbon uptake is expected to be offset by soil gas fluxes) are most beneficial to the overall carbon sequestration of plantation forests.

The overall lower CO$_2$ and N$_2$O fluxes on the plantation suggest that soil C and N cycling rates on this plantation are lower than in the adjacent forest. Mixing of dissimilar litter has been found to increase decomposition rates with the same species (Hattenschwiler and Jorgensen, 2010), suggesting that decomposition should be faster with higher diversity. This could explain the reduced CO$_2$ fluxes on the plantation, but not the reduced N$_2$O fluxes, since litter decomposition mostly affects soil CO$_2$ but not N$_2$O fluxes, as we found during a small litter removal experiment (section 3.2). Compared with primary forests, young plantations have been found to have lower rates of C and N cycling, due to the reduced stand density (Murphy et al., 2008), soil moisture, C pools, organic-N inputs, and decomposition rates (Silver et al., 2005). Difference in soil properties between the forest and plantation confirms that reduced stand density and lack of canopy stratification can lead to higher soil temperatures and lower %WFPS values (Murphy et al., 2008). The higher bulk density on the plantation is similar to local
pasture and cropland values (Wick et al., 2005), which suggests that significant compaction occurred and that tree root densities may be lower on plantations. Smith et al. (1998; 2002) and Boussougou et al. (2010) found C and N cycling rates and bulk densities similar to a nearby forest site in older (20-30 yr old) monoculture plantation plots in Curu-una, ~50km east of Santarem, and Canada, respectively. These plantations were established on newly cleared lands and were not exposed to several cycles of plantation or agricultural management.

4.2 Species differences in monoculture

We measured species differences (P<0.001) for all the parameters measured on the plantation. The soil parameters were only measured to 5 cm depth, which is where tree species have most influence on soil properties (Montagnini and Sancho, 1990; Smith et al., 1998; Russell et al., 2010). The large differences suggest a strong differential influence of native tree species on soil properties and gas fluxes in the clay-rich, upland soils of the Amazon basin.

Our results indicate that tree species have strongly differing growth rates and can influence soil greenhouse gas fluxes and as such this information should be included in the decision making process for plantation design. This is consistent with (Murphy et al., 2008; Brechet et al., 2009; Russell et al., 2010) who also found that tree growth and soil CO₂ fluxes on tree plantations were influenced by tree species. The species differences observed for standing biomass and CO₂ flux were well within the range
measured in other tropical plantations (Murphy et al., 2008; Brechet et al., 2009; Russell et al., 2010). Though we did not conduct a full carbon balance analysis at the plantation, our results indicate that different species can have large differences in the overall impact on climate change mitigation (Table 3). Furthermore, the data for the different greenhouse gases suggests that CO$_2$ exchange has the greatest potential impact, followed by N$_2$O and then CH$_4$ (Table 3). N$_2$O has the added concern of the ozone destruction in the stratosphere, which is most likely for tropical emissions since the mixing between the troposphere and stratosphere is strongest in the tropics.

In plantation and agroforestry applications, N-fixing legume species are beneficial for carbon sequestration since they generally are fast growing species, increase productivity of other species, and are less sensitive to soil fertility (Piotto, 2008; Palm et al., 2010). In our case, the three legume species all had the highest biomass on the plantation, their biomass was even greater than the forest sites (Table 3). However, legumes can have a positive feedback to climate change, since both in tropical forests and plantations, legumes have been shown to stimulate soil N$_2$O fluxes (Erickson et al., 2001; Palm et al., 2002; Asner et al., 2006; Dick et al., 2006; Arai et al., 2008; Hergoualc'h et al., 2008; Palm et al., 2010). This increase has invariably been linked to the N-fixing capability of legumes. We found all legumes on the plantation to be nodulated and were surprised by the low N$_2$O fluxes associated with legume species on the plantation (Table 3 and 5). Low N$_2$O fluxes were paired with low %WFPS on the legume plots, which most likely causes the low N$_2$O fluxes. However, why would
Legumes lower the soil moisture content? Legumes have been found to have relatively high water use efficiency (Cernusak et al., 2007). Higher growth rates and stand densities could create a higher water demand per unit soil volume. Furthermore, the *S. chrysophyllum* plot location at the edge of the plantation, could have created more canopy openness and have led to increased evaporative water loss, which was evident from mortality of several edge trees along the road. Both other legume plots (*H. excelsum* and *C. multijuga*) are centrally located in the plantation and both had full crowns during the sampling times.

Though much less likely, other potential causes for reduced N$_2$O fluxes on legume plots are associated with the need to fix nitrogen in the depleted soils of a plantation. All legume species on the plantation were strongly nodulated (observed during soil sampling), whereas they are only poorly or not nodulated in the forest. N$_2$ fixation is known to be a highly C and P intensive process (Davidson 2008) and as such could inhibit microbial populations through reduced carbon allocation to the rhizosphere. Many legumes produce leaves with high polyphenol concentrations, which bind N-compounds during the decomposition process (Palm and Sanchez, 1990) and thus inhibit the use of carbon compounds by soil decomposers (Hattenschwiler and Jorgensen, 2010). Therefore, it is not unlikely that N$_2$O fluxes on pure legume plots are lower than in mixed plots (Niklaus et al., 2006) or diverse forests. Likewise, most agroforestry studies involving legumes (Dick et al., 2001; Corre et al., 2006; Dick et al., 2006; Arai et al., 2008; Veldkamp et al., 2008; Palm et al., 2010) show an increase in N$_2$O
fluxes associated with the presence of legumes. Legume species in mixed silviculture experiments increase the productivity of the other species (Piotto, 2008), but generally do not do as well themselves. Thus on mixed plantations legumes could cause a positive carbon uptake feedback which leads to increased $N_2O$ production, whereas in isolation, legumes on poor soils invest much of their carbon in nitrogen fixation, which leaves soil microbial populations starved for carbon and thus lower $N_2O$ fluxes.

4.3 Predictive capability of plantation for tree growth and soil properties in forest settings

The different rank order of tree species mean $N_2O$ fluxes in the forest and on the plantation demonstrates that, except for the growth rate, little inference about species effects can be made from the plantation to the forest and vice versa. As far as we know, besides the leaf chemistry measurements by Hattenschwiler et al. (2008), no previous study has compared the same species in a plantation and neighboring forest. Most studies compare the species effects on the plantation with mean forest values (e.g., Smith et al. (1998)), which presumes interference by other species in diverse forests. Unless we test species effects in silviculture and forests little knowledge will be gained about how species interactions change individual species effects.

Lack of predictability between the plantation and the forest soil gas fluxes and properties most likely is the result of effect mixing in the forest. This has been observed in mixed species plantations (Kelty, 2006; Niklaus et al., 2006; Murphy et al., 2008),
where little relationship between the species associated soil differences found in monoculture persisted in the more diverse forest (max 6 species). Our species rank order difference for N$_2$O between forest and plantation for all soil factors appears to be in conflict with Hattenschwiler et al. (2008), who found the same rank order of leaf chemical properties (C, N, and P composition) of four tree species in a plantation and nearby forest in French Guiana. This suggests that tree species experiencing similar climate and soil conditions have a similar nutrient demand and litter chemistry deposition, thus should have predictable soil N$_2$O fluxes (e.g. decomposition, nutrient release, etc.). Lack of this predictability between the plantation and forest at our site in Brazil suggests that trees influence soil N$_2$O fluxes through other mechanisms than decomposition or nutrient acquisition.

4.4 Effects of climate and vegetation drivers on soil processes on the plantation vs. forest

Tree species, like the climate and soil variables clearly have a strong influence on soil gas fluxes. Though many researchers have investigated the effects of climate and soil properties on soil gas fluxes (Breuer et al., 2000; Butterbach-Bahl et al., 2004; Keller et al., 2005; Sotta et al., 2007), this has not been done while including species. Tree species influence on soil gas fluxes is mainly related to root activity and litter dynamics (Valverde-Barrantes, 2007), since litter and roots both contribute to the overall soil CO$_2$ flux and are the main form of contact between trees and soils. Murphy et al. (2008) used path analyses to relate tree biomass, crown mass, and root mass with soil
temperature, moisture, and CO$_2$ flux on the Sardinilla plantation in Panama. They concluded that CO$_2$ fluxes on a tropical plantation were most strongly affected by crown volume and its effects on soil climate variables. Although we found that aboveground biomass did affect soil moisture, it was the soil bulk density that had the greatest influence on soil CO$_2$ flux on the plantation. In the forest, tree biomass and growth appeared to correlate with soil bulk density, though they both did have a positive influence on the CO$_2$ flux as well. The discrepancy between the paths and their strengths in our study and (Murphy et al., 2008), is most likely due to the age difference of the two plantations. At the time of their measurements, the Sardinella plantation was only less than six years old with tree heights up to 10m, whereas the Belterra plantation was ~30 years old with tree heights up to 35m during our measurements. The age and canopy height, together with understory clearing, caused the soil to be less protected by the canopy on the Belterra plantation, and therefore the biomass had less influence on both soil temperature and moisture.
5. Conclusions

Our study combining monoculture plantation plots and diverse forest sites on texturally similar soil has revealed that soil gas fluxes and properties are strongly dependent on the planted tree species in monoculture plantations and less so in the diverse forest. Only for soil N\(_2\)O fluxes we found species effects in both forest and plantation, though relative differences have little predictive capacity for tree species influence in diverse forests. N-fixing legume species provide an important role by returning nitrogen in the growth of secondary forests, especially on abandoned farmland, which is depleted in nitrogen. Though implicated in increased N\(_2\)O fluxes, legumes on clay-rich, terra-firme soils appear to have a negative influence on soil N\(_2\)O fluxes, most likely through greater water use. Although native species are the minority of species planted in plantations on abandoned farm-land (FAO, 2010), the potential carbon sequestration benefit of native tree species should be taken into consideration when plantations are planned.
Acknowledgements

The authors thank the LBA Santarem and EMBRAPA Belterra offices for logistic support and Francisco Alves Freitas Neto, Cleuton Pereira, Jackson da Silva, Marcello da Silva Feitoso, Felipe Saita, and Nilson de Souza Carvalho, for their invaluable help in the field and lab. The research was conducted with funding through a U.S. Forest Service grant to MK and a NSF-PIRE fellowship to JvH.
References


Table 1. Site locations and mean soil properties and gas fluxes (letters denote significant difference P<0.01, within columns).

<table>
<thead>
<tr>
<th>Plantation</th>
<th>Coordinates</th>
<th>pH</th>
<th>% Sand</th>
<th>Soil T °C</th>
<th>BD (g cm⁻³)</th>
<th>%WFPS</th>
<th>CO₂ mg·C m⁻² h⁻¹</th>
<th>N₂O μg·N m⁻² h⁻¹</th>
</tr>
</thead>
<tbody>
<tr>
<td>Belterra (174)</td>
<td>2.66S 125.07W</td>
<td>3.55±0.02&lt;sup&gt;ab&lt;/sup&gt;</td>
<td>3.6±0.4&lt;sup&gt;d&lt;/sup&gt;</td>
<td>25.7±0.06&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.91±0.01&lt;sup&gt;a&lt;/sup&gt;</td>
<td>60.7±1.4&lt;sup&gt;c&lt;/sup&gt;</td>
<td>212±6</td>
<td>26.2±2.2&lt;sup&gt;c&lt;/sup&gt;</td>
</tr>
<tr>
<td>Forest Clay</td>
<td>Km67 (190)</td>
<td>2.86S 125.04W</td>
<td>3.67±0.06&lt;sup&gt;a&lt;/sup&gt;</td>
<td>5.4±1.3&lt;sup&gt;d&lt;/sup&gt;</td>
<td>24.8±0.03&lt;sup&gt;d&lt;/sup&gt;</td>
<td>0.72±0.01&lt;sup&gt;c&lt;/sup&gt;</td>
<td>58.5±1.1&lt;sup&gt;c&lt;/sup&gt;</td>
<td>239±7</td>
</tr>
<tr>
<td>Km72 (80)</td>
<td>2.91S 125.04W</td>
<td>3.45±0.03&lt;sup&gt;b&lt;/sup&gt;</td>
<td>1.2±0.4&lt;sup&gt;d&lt;/sup&gt;</td>
<td>25.5±0.05&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.72±0.02&lt;sup&gt;c&lt;/sup&gt;</td>
<td>70.9±1.4&lt;sup&gt;b&lt;/sup&gt;</td>
<td>243±10</td>
<td>44.4±3.7&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
<tr>
<td>Km83 (72)</td>
<td>3.02S 125.03W</td>
<td>3.59±0.03&lt;sup&gt;ab&lt;/sup&gt;</td>
<td>17.5±2.6&lt;sup&gt;c&lt;/sup&gt;</td>
<td>25.7±0.09&lt;sup&gt;ab&lt;/sup&gt;</td>
<td>0.81±0.02&lt;sup&gt;b&lt;/sup&gt;</td>
<td>83.3±1.2&lt;sup&gt;a&lt;/sup&gt;</td>
<td>228±15</td>
<td>107±8&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td><strong>Forest-Plantation comparison using Welch ANOVA equal means test</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>R&lt;sup&gt;²&lt;/sup&gt;</td>
<td>0.07</td>
<td>0.38</td>
<td>0.26</td>
<td>0.29</td>
<td>0.02</td>
<td>0.30</td>
<td></td>
<td></td>
</tr>
<tr>
<td>F-ratio</td>
<td>6.9</td>
<td>93.9</td>
<td>53.6</td>
<td>62.1</td>
<td>3.3</td>
<td>73.4</td>
<td></td>
<td></td>
</tr>
<tr>
<td>P &gt; F</td>
<td>0.0002</td>
<td>&lt;0.0001</td>
<td>&lt;0.0001</td>
<td>&lt;0.0001</td>
<td>0.02</td>
<td>&lt;0.0001</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Family</td>
<td>Genus</td>
<td>Species</td>
<td>Authority</td>
<td>Common name</td>
<td>Forest</td>
<td>Plantation</td>
<td></td>
<td></td>
</tr>
<tr>
<td>--------------</td>
<td>---------------</td>
<td>---------------</td>
<td>--------------------</td>
<td>----------------------</td>
<td>--------</td>
<td>------------</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Anacardiaceae</td>
<td><em>Astronium</em></td>
<td><em>lecointei</em></td>
<td>Ducke</td>
<td>Aroeira</td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Araliaceae</td>
<td><em>Schefflera</em></td>
<td><em>morototoni</em></td>
<td>(Aubl.) Maguire</td>
<td>Morototo</td>
<td></td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Caryocaraceae</td>
<td><em>Caryocar</em></td>
<td><em>villosum</em></td>
<td>(Aubl.) Pers</td>
<td>Piquiá</td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fabaceae (Caes.)</td>
<td><em>Chamaecrista</em></td>
<td><em>xinguensis</em></td>
<td>(Ducke) H.S.Irwin&amp;Barneby</td>
<td>Coração de negro</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fabaceae (Caes.)</td>
<td><em>Copaifera</em></td>
<td><em>mulijuga</em></td>
<td>Hayne</td>
<td>Copaíba</td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fabaceae (Caes.)</td>
<td><em>Sclerolobium</em></td>
<td><em>chrysophyllum</em></td>
<td>Poepp.</td>
<td>Tachi vermelho</td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fabaceae (Mim.)</td>
<td><em>Psuedopiptadenia</em></td>
<td><em>psilostachya</em></td>
<td>(Benth.) G.P.Lewis&amp;M.P.Lima</td>
<td>Fava folha fina</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fabaceae (Pap.)</td>
<td><em>Hymenolobium</em></td>
<td><em>excelsum</em></td>
<td>(Ducke) Benth</td>
<td>Angelim da mata</td>
<td></td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lecythidaceae</td>
<td><em>Bertholletia</em></td>
<td><em>excelsa</em></td>
<td>Humb.&amp;Bonpl.</td>
<td>Castanha do Pará</td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lecythidaceae</td>
<td><em>Couratari</em></td>
<td><em>stellata</em></td>
<td>Aubl.</td>
<td>Tauári</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lecythidaceae</td>
<td><em>Lecythis</em></td>
<td><em>lurida</em></td>
<td>(Miers) Mori</td>
<td>Jarana</td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Meliaceae</td>
<td><em>Carapa</em></td>
<td><em>guianensis</em></td>
<td>Aubl.</td>
<td>Andiroba</td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sapotaceae</td>
<td><em>Manilkara</em></td>
<td><em>huberi</em></td>
<td>(Ducke) Chev.</td>
<td>Maçaranduba</td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sapotaceae</td>
<td><em>Pouteria</em></td>
<td><em>reticulate</em></td>
<td>(Engl.) Eyma</td>
<td>Abiu</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Vochysiaceae</td>
<td><em>Erisma</em></td>
<td><em>uncinatum</em></td>
<td>Warm.</td>
<td>Quarubaranha</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Vochysiaceae</td>
<td><em>Vochysia</em></td>
<td><em>maxima</em></td>
<td>Ducke</td>
<td>Quaruba verdadeira</td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Tree species were initially identified in 1999 along the km 67 transects by Nelson A. Rosa from the Museu Emilio Goeldi in Belém, Pará, where voucher specimens are stored in the museum collection. During our field campaigns, Nilson de Souza Carvalho (EMBRAPA, Belterra, Pará) conducted all the tree identifications. All tree species are also described in (Parotta et al., 1995).
Table 3. Vegetation mass and carbon equivalent* fluxes from plantation and forest.

<table>
<thead>
<tr>
<th>Plantation Species</th>
<th>Biomass MgC ha(^{-1})</th>
<th>CO(_2) MgC ha(^{-1}) y(^{-1})</th>
<th>CH(_4) MgC ha(^{-1}) y(^{-1})</th>
<th>N(_2)O MgC ha(^{-1}) y(^{-1})</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. lecontei</td>
<td>93.6</td>
<td>21.5(_{3.3}^{1.9})</td>
<td>0.02(_{0.02}^{0.02})</td>
<td>0.33(_{0.08}^{0.11})</td>
</tr>
<tr>
<td>B. excelsa</td>
<td>182.5</td>
<td>18.2(_{1.2}^{1.3})</td>
<td>-0.02(_{0.01}^{0.01})</td>
<td>0.34(_{0.05}^{0.06})</td>
</tr>
<tr>
<td>C. guinanensis</td>
<td>145.1</td>
<td>21.9(_{1.9}^{2.1})</td>
<td>0.10(_{0.04}^{0.04})</td>
<td>0.85(_{0.15}^{0.18})</td>
</tr>
<tr>
<td>C. multijuga</td>
<td>290.2</td>
<td>15.9(_{0.9}^{1.0})</td>
<td>-0.11(_{0.02}^{0.02})</td>
<td>0.28(_{0.05}^{0.05})</td>
</tr>
<tr>
<td>C. villosum</td>
<td>134.5</td>
<td>20.1(_{1.1}^{1.2})</td>
<td>-0.04(_{0.03}^{0.03})</td>
<td>0.37(_{0.05}^{0.05})</td>
</tr>
<tr>
<td>H. excelsum</td>
<td>302.3</td>
<td>18.7(_{1.9}^{2.1})</td>
<td>-0.01(_{0.02}^{0.02})</td>
<td>0.09(_{0.02}^{0.02})</td>
</tr>
<tr>
<td>L. lurida</td>
<td>45.9</td>
<td>14.9(_{1.0}^{1.1})</td>
<td>-0.03(_{0.01}^{0.01})</td>
<td>0.23(_{0.03}^{0.03})</td>
</tr>
<tr>
<td>M. huberi</td>
<td>151.0</td>
<td>24.2(_{1.6}^{1.7})</td>
<td>-0.01(_{0.03}^{0.03})</td>
<td>0.33(_{0.09}^{0.12})</td>
</tr>
<tr>
<td>S. chrysophyllum</td>
<td>211.8</td>
<td>17.6(_{1.2}^{1.3})</td>
<td>-0.08(_{0.04}^{0.05})</td>
<td>0.09(_{0.03}^{0.04})</td>
</tr>
<tr>
<td>V. maxima</td>
<td>114.8</td>
<td>17.3(_{0.4}^{1.3})</td>
<td>-0.04(_{0.02}^{0.02})</td>
<td>0.33(_{0.03}^{0.04})</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Sites</th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Plantation</td>
<td>175±27</td>
<td>18.57</td>
<td>-0.03</td>
<td>0.29</td>
</tr>
<tr>
<td>Forest</td>
<td>20.82</td>
<td>-0.1</td>
<td>0.86</td>
<td></td>
</tr>
<tr>
<td>km 67</td>
<td>197±11.6</td>
<td>20.94</td>
<td>0.96</td>
<td></td>
</tr>
<tr>
<td>km 72</td>
<td>212±9.7</td>
<td>21.29</td>
<td>0.49</td>
<td></td>
</tr>
<tr>
<td>km 83</td>
<td>NA</td>
<td>19.97</td>
<td>1.19</td>
<td></td>
</tr>
</tbody>
</table>

*Carbon equivalent fluxes were calculated based on the difference in global warming potential (IPCC, 2007) of the gases (1, 23, 296, for CO\(_2\), CH\(_4\), and N\(_2\)O, respectively).
Table 4. Fraction of flux variance explained by species and soil variables.

<table>
<thead>
<tr>
<th>CO₂</th>
<th>Species</th>
<th>pH</th>
<th>Soil T °C</th>
<th>BD (g cm⁻³)</th>
<th>% SM</th>
<th>%WFPS</th>
<th>MLR ¹</th>
</tr>
</thead>
<tbody>
<tr>
<td>Plantation</td>
<td>0.12*</td>
<td>0.09**</td>
<td>0.03*</td>
<td>0.17****</td>
<td>0.06**</td>
<td>0.01</td>
<td>Sp+BD 0.2</td>
</tr>
<tr>
<td>Forest Clay</td>
<td>0.07</td>
<td>0.01</td>
<td>0.11****</td>
<td>0.09****</td>
<td>0.04***</td>
<td>0.06****</td>
<td>Sp+T+BD 0.2</td>
</tr>
<tr>
<td>Km 67</td>
<td>0.09</td>
<td>0.01</td>
<td>0.07**</td>
<td>0.05**</td>
<td>0.01</td>
<td>0.06***</td>
<td>T+BD 0.12</td>
</tr>
<tr>
<td>Km 72</td>
<td>0.16</td>
<td>0.00</td>
<td>0.05</td>
<td>0.17***</td>
<td>0.04</td>
<td>0.15**</td>
<td>Sp+BD 0.25</td>
</tr>
<tr>
<td>Km 83</td>
<td>0.14</td>
<td>0.03</td>
<td>0.34****</td>
<td>0.17**</td>
<td>0.18**</td>
<td>0.02</td>
<td>Sp+T+M 0.41</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>N₂O</th>
<th>Species</th>
<th>pH</th>
<th>Soil T °C</th>
<th>BD (g cm⁻³)</th>
<th>% SM</th>
<th>%WFPS</th>
<th>MLR ¹</th>
</tr>
</thead>
<tbody>
<tr>
<td>Plantation</td>
<td>0.34****</td>
<td>0.07*</td>
<td>0.04*</td>
<td>0.08***</td>
<td>0.10****</td>
<td>0.01</td>
<td></td>
</tr>
<tr>
<td>Forest Clay</td>
<td>0.17****</td>
<td>0.03*</td>
<td>0.00</td>
<td>0.02*</td>
<td>0.00</td>
<td>0.05****</td>
<td>Sp+W 0.11****</td>
</tr>
<tr>
<td>Km 67</td>
<td>0.17**</td>
<td>0.06</td>
<td>0.00</td>
<td>0.01</td>
<td>0.01</td>
<td>0.06**</td>
<td>Sp+%W 0.1</td>
</tr>
<tr>
<td>Km 72</td>
<td>0.26**</td>
<td>0.15**</td>
<td>0.01</td>
<td>0.04</td>
<td>0.00</td>
<td>0.05</td>
<td></td>
</tr>
<tr>
<td>Km 83</td>
<td>0.11</td>
<td>0.01</td>
<td>0.14**</td>
<td>0.00</td>
<td>0.00</td>
<td>0.01</td>
<td></td>
</tr>
</tbody>
</table>

¹ MLR stands for Multiple Linear Regression, which was conducted through a stepwise module in JMP. Within the column Sp, BD, T, M, and W stand for species, bulk density, temperature, moisture, and %WFPS, respectively. ²After removal of one outlier, with outlier R²<0.01.*,**,***,**** denote significance at P<0.05, 0.01, 0.001, and 0.0001 levels.
Table 5. Effects of legume tree species on soil parameters on the plantation and in the forest.

<table>
<thead>
<tr>
<th></th>
<th>Growth cm y(^{-1})</th>
<th>pH</th>
<th>Soil T °C</th>
<th>BD (g cm(^{-3}))</th>
<th>WFPS %</th>
<th>CO(_2) mg-C m(^{-2}) h(^{-1})</th>
<th>N(_2)O μg-C m(^{-2}) h(^{-1})</th>
<th>CH(_4) μg-C m(^{-2}) h(^{-1})</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Plantation</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Non-legume</td>
<td>0.56±0.09</td>
<td>3.57±0.03</td>
<td>25.8±0.1</td>
<td>0.91±0.01</td>
<td>61.8±0.9</td>
<td>216(^{-7})</td>
<td>32.1(^{2.5})</td>
<td>-13.7(^{4.1})</td>
</tr>
<tr>
<td>Legume</td>
<td>1.29±0.12</td>
<td>3.47±0.02</td>
<td>25.6±0.1</td>
<td>0.94±0.01</td>
<td>55.2±2.0</td>
<td>198(^{10})</td>
<td>10.8(^{2.2})</td>
<td>-35.6(^{10.4})</td>
</tr>
<tr>
<td>Student’s t</td>
<td>4.9</td>
<td>-2.8</td>
<td>-1.5</td>
<td>1.9</td>
<td>-3.1</td>
<td>-1.5</td>
<td>-5.4</td>
<td>-1.9</td>
</tr>
<tr>
<td>two sided P</td>
<td>0.007</td>
<td>0.006</td>
<td>0.15</td>
<td>0.06</td>
<td>0.005</td>
<td>0.13</td>
<td>&lt;0.0001</td>
<td>0.09</td>
</tr>
<tr>
<td><strong>Forest Clay</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Non-legume</td>
<td>0.59±0.09</td>
<td>3.58±0.02</td>
<td>25.1±0.1</td>
<td>0.73±0.01</td>
<td>66.6±0.6</td>
<td>239(^{6})</td>
<td>76.6(^{3.2})</td>
<td>-53.8(^{6.8})</td>
</tr>
<tr>
<td>Legume</td>
<td>0.69±0.49</td>
<td>3.40±0.05</td>
<td>25.1±0.1</td>
<td>0.75±0.02</td>
<td>66.6±1.1</td>
<td>230(^{11})</td>
<td>80.2(^{6.7})</td>
<td>-43.7(^{10.4})</td>
</tr>
<tr>
<td>Student’s t</td>
<td>0.4</td>
<td>-3.1</td>
<td>-0.5</td>
<td>0.9</td>
<td>-0.1</td>
<td>-0.7</td>
<td>0.5</td>
<td>0.5</td>
</tr>
<tr>
<td>two sided P</td>
<td>0.71</td>
<td>0.004</td>
<td>0.63</td>
<td>0.80</td>
<td>0.95</td>
<td>0.48</td>
<td>0.62</td>
<td>0.60</td>
</tr>
</tbody>
</table>
Figure captions.

Figure 1. Map of Brazil with site locations and detailed transect information for the established forest sites in the Tapajos National Forest (TNF) bound by the BR-163 on the east and Tapajos river on the west. The plantation is highlighted on the top left, with the letters denoting the different species plots (AL = *A. lecontei*, BE = *B. excelsa*, CG = *C. guinanensis*, CM = *C. Multijuga* (legume), CV = *C. villosum*, HE = *H. Excelsum* (legume), LL = *L. Lurida*, MH = *M. Huberi*, SC = *S. Chrysophyllum* (legume), and VM = *V. Maxima*).

Figure 2. Box plots by species of all measured variables both in the forest (grey filled boxes) and plantation (open boxes). ANOVA results are represented by both the $R^2$ (variance explained) and P-value. Stars above or below the box and whiskers indicate variables that differ between forest and plantation (*=0.05, **=0.01, ***=0.001, and ****=0.0001). The capital letter next to the boxes indicate species differences ($\ddagger$=0.01); lower case letters indicate species differences within the plantation.

Figure 3. Semi-variogram plots of bulk density (BD), soil moisture (WFPS), CO$_2$ and N$_2$O flux for both the forest (left) and plantation (right). The plots were generated with the geoR package in R, using least squares fit to the data. The plots demonstrate that all parameters contain very high nugget variance and a small range, indicating that the analysis were independent at distances <2 m, which renders most samples independent.

Figure 4. Best SEM models of the environmental factors on soil a) CO$_2$ and b) N$_2$O fluxes on the plantation and c) CO$_2$ and d) N$_2$O in the forest. Models were selected based on
BIC and RSME values and addition of paths was decided based on the modification indices. Values next to the arrows indicate the unstandardized coefficients and the width of the arrows indicates the statistical significance of the path (dotted line $P>0.5$, dashed line $0.2<P<0.5$, line $0.05<P<0.2$, thick line $0.01<P<0.05$, thicker line $P<0.01$, thickest lines $P<0.001$). The models suggest that the main drivers for CO$_2$ flux variability are ST and BD for both sites, whereas either ST (plantation) or WFPS (forest) are the main drivers for N$_2$O flux variability.

Figure 5. SEM diagrams like in figure 4 with the inclusion of biological parameters (biomass: a-d and tree growth rate: e-f) for the plantation (a and b) and the forest (c-f). Models were selected based on BIC and RSME values and addition of paths was decided based on the modification indices. Values next to the arrows indicate the unstandardized coefficients and the width of the arrows indicates the statistical significance of the path (dotted line $P>0.5$, dashed line $0.2<P<0.5$, line $0.05<P<0.2$, thick line $0.01<P<0.05$, thicker line $P<0.01$, thickest lines $P<0.001$). The models suggest that tree biomass has much greater influence on the soil gas fluxes in the forest than the plantation and that tree growth rate has a strong direct influence on soil N$_2$O fluxes in the forest.
Figure 1.
Figure 3

Forest

Plantation

BD (g cm\(^{-3}\))

%WFPS

\(\text{CO}_2\) (mg C m\(^{-2}\) h\(^{-1}\))

\(\text{N}_2\text{O}\) (g N m\(^{-2}\) h\(^{-1}\))

Distance (m)
Figure 4

A. Forest N\textsubscript{2}O = -0.5*BD + 0.02*WFPS + 0.1*ST

B. Plantation N\textsubscript{2}O = -1*BD + 0.01*WFPS + 0.5*ST

C. Forest CO\textsubscript{2} = -0.74*BD - 0.001*WFPS + 0.24*ST

D. Plantation CO\textsubscript{2} = -0.74*BD - 0.001*WFPS + 0.24*ST

Chi\textsuperscript{2} = 5.8
Pr>Chi\textsuperscript{2} = 0.12
Adj Goodness Fit = 0.97
RMSEA = 0.05 (NA, 0.12)
BIC = -11.7

Chi\textsuperscript{2} = 3.0
Pr>Chi\textsuperscript{2} = 0.38
Adj Goodness Fit = 0.98
RMSEA = 0.006 (NA, 0.09)
BIC = -14.5

Chi\textsuperscript{2} = 1.6
Pr>Chi\textsuperscript{2} = 0.81
Adj Goodness Fit = 0.99
RMSEA = 0 (NA, 0.8)
BIC = -14.4

Chi\textsuperscript{2} = 1.0
Pr>Chi\textsuperscript{2} = 0.79
Adj Goodness Fit = 0.99
RMSEA = 0 (NA, 0.8)
BIC = -14.4
Figure 5

A

B

C

D

E

F

Chi² = 0.99
Pr>Chi² = 0.8
Adj Goodness Fit = 0.98
RSMEA = 0 (NA, 0.09)
BIC = -13.5

Chi² = 2.0
Pr>Chi² = 0.73
Adj Goodness Fit = 0.98
RSMEA = 0 (NA, 0.10)
BIC = -17.2

Chi² = 2.1
Pr>Chi² = 0.56
Adj Goodness Fit = 0.99
RSMEA = 0 (NA, 0.09)
BIC = -14.8

Chi² = 5.0
Pr>Chi² = 0.41
Adj Goodness Fit = 0.98
RSMEA = 0 (NA, 0.09)
BIC = -23.3

Chi² = 3.1
Pr>Chi² = 0.54
Adj Goodness Fit = 0.98
RSMEA = 0 (NA, 0.08)
BIC = -19.5

Chi² = 7.7
Pr>Chi² = 0.26
Adj Goodness Fit = 0.97
RSMEA = 0 (NA, 0.10)
BIC = -25.2
APPENDIX D

FOREST GROWTH PREDICTS TROPICAL SOIL N₂O FLUXES

Joost van Haren

Raimundo Cosme de Oliveira Jr

Michael Keller

Scott Saleska

Advanced draft to be submitted to Proceedings of the national Academy of Sciences
Forest growth predicts tropical soil $\text{N}_2\text{O}$ fluxes

Joost L.M. van Haren$^{1,4*}$, Raimundo Cosme de Oliveira$^{2}$, Changshen Li$^{3}$, Steve Frolking$^{3}$, Michael Keller$^{3}$, Ruth Varner$^{3}$, and Scott Saleska$^{4}$.

Advanced draft to be send to Nature or PNAS

Author affiliation:

$^{1}$Dept. Soil, Water, and Environmental Science, University of Arizona, Tucson, AZ, USA

$^{2}$EMBRAPA Amazônia Oriental, Santarém, Pará, Brazil

$^{3}$University of New Hampshire, Durham, NH, USA

$^{4}$Dept. Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ, USA

Corresponding author: Joost van Haren, Biosciences West, 1041 East Lowell Street, Tucson, AZ 85721, USA; ivanhare@email.arizona.edu, (520) 626-5838, Fax: (520) 621-9190.
Abstract

The high spatial and temporal variability of soil N\textsubscript{2}O fluxes, which process based models have not managed to fully describe, has impeded their extrapolation from chamber to whole ecosystem. Our work to determine the spatial and temporal variability of soil gas fluxes in the Tapajos National Forest in central Amazonia, Brazil, found that soil N\textsubscript{2}O fluxes are spatially and temporally highly correlated with overall forest growth. We hypothesize that the mechanism for this correlation is through belowground carbon allocation by trees. Trees are the main source of carbon to the soil microbial community and sugar addition experiments have demonstrated that soil communities are carbon limited. Extrapolation to a wide variety of forest inventory plots around the Amazon basin yields a basin wide N\textsubscript{2}O flux of 2.6 kg-N ha\textsuperscript{-1} y\textsuperscript{-1}. Application of a process based model (PnET-DNDC) to our datasets reproduces the relationship between wood growth and N\textsubscript{2}O fluxes.
Introduction

$\text{N}_2\text{O}$, an important greenhouse gas and an important contributor to ozone destruction$^{1,2}$, has increased exponentially since the onset of the industrial revolution$^3$. Tropical forest soils represent the largest natural source of $\text{N}_2\text{O}$ to the atmosphere$^4$. However, their contribution to the global budget still remains poorly quantified$^5$, due to the few measurements of forest $\text{N}_2\text{O}$ fluxes in tropical regions$^5$ and the highly variable nature of $\text{N}_2\text{O}$ production and consumption through denitrification$^6$. In soils, $\text{N}_2\text{O}$ is produced through nitrification and denitrification by microorganisms$^7$. Substrate limitation (ammonia, nitrate and labile carbon), oxygen and water concentration, pH, and gas transport greatly affect the resulting $\text{N}_2\text{O}$ flux$^8$–$^{10}$. In tropical forests, nitrogen limitation and pH generally decrease with soil age, though phosphorous might become limiting to microbial growth, increasing $\text{N}_2\text{O}$ fluxes on older soils. Little is known about carbon availability in tropical soils, though sugar additions generally lead to large increases in $\text{N}_2\text{O}$ fluxes –irrespective of nutrient availability$^{11,12}$, which suggests that carbon is limiting soil $\text{N}_2\text{O}$ production in tropical soils.

Several models have been proposed and tested to extrapolate soil $\text{N}_2\text{O}$ fluxes from flux-chamber to ecosystem, though none of them explicitly includes tree growth or ecosystem productivity. Simple correlation approaches based on ecosystem CO$_2$ flux$^{13}$ or soil C/N ratio$^{14}$ appear to work well under conditions where mineralization and nitrification dominate$^{15,16}$. They fail to explain $\text{N}_2\text{O}$ flux variability in tropical forests on
clay-rich soils during the wet season when denitrification is the dominant N$_2$O production process. Li et al.\textsuperscript{17} developed a process based model (PnET-DNDC) for temperate forests, which combines above and below ground forest ecosystem dynamics (forest growth submodel, Photosynthesis-Evaporation model, PnET) with soil biogeochemistry (the Denitrification-Decomposition submodel model, DNDC). Their model structure is such that tree growth regulates N uptake and leaf litter production. It allows for competition between trees and microbes for ammonia and nitrate, thus increased tree growth can negatively impact N$_2$O production by reduction of substrate. On the other hand, increased growth produces more litter and as such potentially increases N$_2$O fluxes, mainly through nitrification.

**Concept**

In this paper we set out to promote tree and forest growth (biomass production) as an explanatory variable for soil N$_2$O fluxes, both on a monthly and annual basis. The main assumptions behind our theory are: 1) plants are the main source of carbon for soil microorganism communities, 2) belowground carbon allocation is a proportion of the downward sap (phloem) carbohydrate flow from leaves, through the stem, to the roots and out into the soil (Figure 1), and 3) below-ground communities are carbon limited. Although, both lichens and cyanobacteria can be important carbon fixing populations in desert ecosystems, their contribution to the overall carbon sequestration in forest ecosystems is very small. Especially in tropical forests the link between labile carbon
availability and soil N\textsubscript{2}O fluxes has been well demonstrated\textsuperscript{11,12,16}. Denitrification is conducted by heterotrophs and they require labile carbon sources for their maintenance and growth (Figure 1). The link between stem growth and below ground carbon allocation is tentative. Below ground carbon allocation has remained very difficult to quantify\textsuperscript{18,19}, though the strong allometric relationships between the above and below ground plant components\textsuperscript{20,21} suggests a predictable regulation of root exudation. However, like the potential of tropical trees to use stored carbon to conduct a full leaf flush\textsuperscript{22}, use of carbon stored in large roots for root exudates could decouple them from the phloem carbon flow.

Light, precipitation, and soil nutrient status are the main regulators of forest growth rates. Though precipitation is relatively abundant, tropical forest growth is highly susceptible to annual precipitation and especially dry season length\textsuperscript{23}. Low growth rates during dry months suggests that phloem transport of carbohydrates from the crown to the stem and roots is limited\textsuperscript{24}, which could be due to water limitation for phloem transport or increased carbon allocation within the crown, to maximize use of increased light availability. Many tree species shed their leaves late wet or early dry season and then flush out new leaves, which can be done based on stored reserves. Forest growth rates are also strongly influenced by soil nutrient content\textsuperscript{25-28}. Although the type of nutrient limitation varies strongly with soil age, mature forests are generally very efficient in recycling limiting nutrients.
Soil pH, oxygen concentration, nutrient status, water content, and labile carbohydrates are the dominant drivers for soil N₂O fluxes. Matson et al.²⁹ tied soil N₂O fluxes to N-mineralization rates across several tropical sites. Though soil pH was found to be the most dominant factor in laboratory incubations and model sensitivity tests, it has remained difficult to demonstrate this sensitivity in the field. Davidson et al.⁹ demonstrated with their ‘hole-in-the-pipe’ model that a significant portion of N₂O flux variability can be explained by a combination of soil water content or %WFPS, soil nutrient content, and labile carbon. Soil moisture at up to 30-40 %WFPS values provides enough water for microbial activity, but when %WFPS values increase beyond saturation (~70% WFPS), moisture mainly provides a barrier for oxygen to reach microsites, where under anaerobic conditions denitrification can occur. If water content increases to a waterlogged state, N₂O fluxes can decrease due to the reduction of N₂O to N₂, the last step of the denitrification pathway. However, in the highly acidic soils of the Amazon basin the end-product of denitrification is predominantly N₂O, since the enzyme N₂O reductase is inhibited at pH<4⁸.

Since most major factors influencing tropical forest growth rates and soil N₂O fluxes are the same, a high covariance between these two aspects of the overall greenhouse gas budget of forests is expected. There is a mechanistic explanation for the covariance, as explained earlier, though establishing the direct links, such as the temporal variability of root exudation will remain a challenge to carbon cycling and biogeochemical research. The covariance between tree growth and N₂O fluxes would not only lead to better forest
greenhouse budget accounting, but it also could lead to more close ties between these factors within the process based models.

**Methods**

We collected soil trace gas fluxes at four forest inventory plot sites in the Tapajos National Forest (TNF), south of Santarem in central Amazonia, Brazil. Forest growth rates were determined based on DBH measurements of all trees greater than 0.1m in diameter. Approximately 1000 trees at km 67 were outfitted with dendrometry bands to measure their growth rates at subannual timescales. Soil gas fluxes were predominantly measured with manual chambers. Either we measured soil gas fluxes several times during the wet season, or they were measured every two weeks by revisiting the same 1 ha with eight manual chambers, which were installed each time. Concurrent soil flux and dendrometry measurements at km 67 allowed us to compare monthly growth rates and N₂O fluxes for a period over 3 years between 2000-2004.

We furthermore collected flux data at three more locations in the TNF and during short campaigns in the transition between wet and dry season at the Rainfor plots in the Caxiuana National Forest and at Reserva Ducke. All these sites also were forest inventory plots and measurements were taking place before, during and after we collected the gas fluxes, and we applied the same allometric relationship to all the demography data. At several sites around Manaus, including Reserva Ducke, soil N₂O
flux measurements were taken previously\textsuperscript{32-34}. To expand our dataset, we searched the literature for sites where soil N\textsubscript{2}O fluxes were measured where forest inventory plots also have been measured (Table 1). When found, we tried to get the original data to make sure that the analyses were identical for all sites. Besides the N\textsubscript{2}O flux measurements, many sites used local allometric equations to calculate wood growth based on DBH measurements. Different allometric approaches can give different mass growth rates, especially when the larger trees are concerned\textsuperscript{35}.

Based on the wet season soil N\textsubscript{2}O fluxes from the TNF, Caxiuana, and Ducke, we developed an exponential relationship between annual and wet season soil N\textsubscript{2}O flux and annual wood growth. To test the validity of this empirical relationship we applied this equation to the Amazon basin-wide annual wood growth rates reported by\textsuperscript{36,37}, who also used allometric methods based on\textsuperscript{38}, though with the inclusion of tree density\textsuperscript{39}. The inclusion of wood density might lead to an overestimation of the annual wood growth rates, because larger trees are often higher density species.

We used several different packages within R to conduct the linear and exponential regressions and Structural Equation Modeling (SEM, see Supplemental material). We simulated wood growth and soil N\textsubscript{2}O fluxes with the PnET-DNDC\textsuperscript{5,17,40} and ForestDNDCTropica\textsuperscript{40,41} models for a couple of years of climate data at our core site in the TNF. Both models have similar below ground parameterization, but use the
Photosynthesis-and-Evapotranspiration (PnET) or Lund-Potsdam-Jund Dynamic Global Vegetation Model (LPJ-DGVM) parameterization for the vegetation components.

Results

The wet season soil $\text{N}_2\text{O}$ fluxes and mean annual growth rate of all trees greater than 10cm DBH in the Tapajos National Forest sites yields a strong positive correlation (Fig. 2). SEM modeling of the monthly $\text{N}_2\text{O}$ fluxes within the Tapajos suggests that the link between tree growth and $\text{N}_2\text{O}$ flux was stronger than %WFPS and $\text{N}_2\text{O}$ flux (Supplemental Figure 2a).

Across east central Amazonia we found a consistent trend between wet season soil $\text{N}_2\text{O}$ fluxes and annual forest growth rates (Fig.2a). Even, when the annual mean fluxes were used, this relationship still held (Fig.2b), though the slope was significantly reduced. We applied the empirically derived annual wood growth vs. mean annual $\text{N}_2\text{O}$ flux to the stem growth data from$^{36}$ and found that predicted soil$\text{N}_2\text{O}$ fluxes are expected to be much higher in the western Amazon basin. Only$^{32}$ measured soil $\text{N}_2\text{O}$ fluxes in the western Amazon basin, though these measurements were only taken during the dry season, and not reflective of the annual $\text{N}_2\text{O}$ flux.

We applied the optimized version of the ForestDNDCTropica model$^{41}$ with biomass, climate, and soil texture to reflect our site. The model did remarkably well for the soil $\text{N}_2\text{O}$ flux, but poorly for wood growth (Table 1). Soil $\text{N}_2\text{O}$ flux changed appropriately with adjustment of the soil texture parameters, but wood growth did not. After initial
calibration of the PnET-DNDC model to our site, our initial runs captured the annual soil 
N$_2$O flux and wood growth variability reasonably well (Table 1), though respiration was 
overestimated by a factor of 2 to 3. Since root exudates are parameterized in the model 
as a fixed fraction of wood growth, the latter can be used as a proxy. Both precipitation 
and soil texture caused an expected change in N$_2$O flux and wood growth, though the 
magnitude was not as extreme as found in the field.

Discussion and conclusions

Our data and modeling support the hypothesis that tree stem growth, most likely 
though the concomitant transport of carbon belowground, can be a main predictor for 
N$_2$O fluxes in the Amazon basin. The overall relationship between forest growth and soil 
N$_2$O fluxes agrees well with the modeled PnET-DNDC results from Australia\textsuperscript{40}, which 
suggest that within the model space there is a positive relationship between overall 
ANPP and soil N$_2$O flux. However, with their model, we could not reproduce a similar 
relationship between wood growth and N$_2$O fluxes for our sites. Further investigation of 
the model will be needed to elucidate the mechanism for this discrepancy. We 
documented a strong correlation between tree growth rates and soil N$_2$O fluxes 
temporally, within one site, across multiple sites within one forest (TNF), and across the 
central-eastern Amazon basin. Furthermore, our PnET-DNDC model results, though not 
without problems, confirm the temporal relationship between wood growth, a 
surrogate measure for root exudates, which is a fixed component of available carbon
allocation, and soil N₂O fluxes. The model breakdown after three years indicates that if nitrogen is limited, the connection between carbon availability and soil N₂O flux breaks down.

The temporal relationship between tree growth and soil N₂O fluxes and the observation that tree growth rates appears to be the strongest predictor for soil N₂O fluxes suggests that root exudation might be more important than previously appreciated. There are several caveats we have to discuss that are related to the temporal measurements of tree growth rates. The use of dendrometer bands to extract tree growth variability within a year is not free of pitfalls. Some dendrometer bands are not responsive enough, at the same time the temporal variability of tree diameter might not reflect actual growth, but a response to changing proportions of sap and hardwood. Most, including ours, sub-annual dendrometry data do not account for these perceived and real growth variations. However, the consistency of the growth vs. flux pattern over the course of three years and across several sites within the Amazon basin, increased confidence in our hypothesis that carbon supply of the soil microorganisms by the trees through allocation of carbon to both the stem and roots drives the high soil N₂O fluxes during the wet season.

All the evidence: 1) covariance between tree growth rate and soil N₂O fluxes and CO₂ fluxes, 2) high N₂O fluxes tied to moist soil conditions, and 3) the relationship between modeled daily root exudates and soil N₂O flux, suggest that trees stimulate soil
microorganisms with phloem derived labile carbon and potentially nitrogen compounds. The direct evidence is very hard to get in natural ecosystems, but there are some possible techniques that can be used to test the labile carbon hypothesis. Hogberg et al.\textsuperscript{42} conducted several girdling experiments, where a narrow strip of bark has been removed from trees in an experimental area. This prevents phloem allocation to the roots and the soil and as such greatly reduces soil respiration. This method cannot distinguish between root mortality and root exudation and as such not very applicable. Phillips et al.\textsuperscript{43} have recently developed methods to directly get at root exudates. Though promising, implementing these methods is not easy and requires whole fine root recovery from the soil matrix, which works reasonably well in sandy soils, but is extremely difficult to achieve in clay-rich soil.

If we assume that our regional analysis of soil \(\text{N}_2\text{O}\) fluxes based on the empirical relationship between wood growth and soil \(\text{N}_2\text{O}\) fluxes applied to the Malhi et al. dataset, we derived a basin wide mean soil \(\text{N}_2\text{O}\) flux of 2.5-3.0 kg-N ha\(^{-1}\) y\(^{-1}\) for the Amazon basin. This estimate exceeds those of other predictions\textsuperscript{41,44,45}, though is considerably lower than Inverse modeling flux estimates (5.5 to 7.0 kg-N ha\(^{-1}\) y\(^{-1}\)) based on airplane measurements\textsuperscript{46}. The previous studies could have underestimated the Amazon basin \(\text{N}_2\text{O}\) flux, which appears the case for the process based model estimate of 0.5-1.0 kg-N ha\(^{-1}\) y\(^{-1}\), which was based on model calibration to three non-Amazonian sites\textsuperscript{5}. We do not expect the \(\text{N}_2\text{O}\) flux indefinitely to increase with increasing wood growth rates, however, or east-to-west increase in soil \(\text{N}_2\text{O}\) flux is consistent with
previous model estimates. Another potential for overestimation are the differences in allometric relations in different regions. Although we used similar allometric equations for all our analysis, the equations might overestimate certain areas relative to others. Nonetheless, by investigating the relationship between tree growth rates and soil $\text{N}_2\text{O}$ fluxes at several spatial and temporal levels we find that one can develop a robust relationship between the two ecosystem parameters. Several aspects still need more attention, in particular we still lack direct evidence for the underlying mechanism that links tree growth and $\text{N}_2\text{O}$ fluxes. In our opinion, most likely candidates are labile root exudates and root turnover in the soil and plant microbe nutrient competition. As mentioned earlier, both are notoriously difficult to determine in remote field settings. Other caveats that will need further attention are the lack of annual temporally detailed flux measurements as were taken in Queensland, Australia$^{47,48}$, the potential issues with inconsistent allometric equations, and large variability in forest growth and $\text{N}_2\text{O}$ fluxes within certain soil type classifications.

The general trend of higher predicted $\text{N}_2\text{O}$ fluxes in the wetter, western Amazon basin suggests that with increasing climate change and likely drying of the Amazon basin, a reduction in forest $\text{N}_2\text{O}$ fluxes is likely. This would have positive implication for stratospheric ozone, but not for climate change feedbacks since the associated carbon loss is expected to be much greater. We strongly suggest that future studies of soil $\text{N}_2\text{O}$ fluxes around the world are conducted within a wider framework of ecological measurements, to provide a more robust understanding of the role of ecology on the
feedbacks to climate change. In particular, N-cycling and N$_2$O trace gas studies in ecosystems prone to anaerobic conditions, such as riparian areas, marshlands, and tropical forests, should either include the aboveground dynamics or choose their study sites where forest inventory infrastructure is already available.
References


Table 1. Annual measured and model predicted wood growth (Mg-C ha\(^{-1}\) y\(^{-1}\)) and N\(_2\)O flux (kg-N ha\(^{-1}\) y\(^{-1}\)) for a clay-rich and sandy site in the Tapajos National Forest, Brazil

<table>
<thead>
<tr>
<th></th>
<th>Measured</th>
<th>PnET-DNDC</th>
<th>ForestDNDC-Tropica</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Wood growth</td>
<td>N(_2)O flux</td>
<td>Wood growth</td>
</tr>
<tr>
<td>Clay-rich</td>
<td>3.4</td>
<td>3.2</td>
<td>3.0</td>
</tr>
<tr>
<td>Sandy</td>
<td>1.7</td>
<td>1.4</td>
<td>1.9</td>
</tr>
</tbody>
</table>
Figure captions:

Figure 1. Conceptual figure of the factors influencing forest growth rate and soil N$_2$O fluxes in tropical forests. The cartoon on the left outlines carbon flow from the atmosphere to soils. The small inset on the roots shows the main areas of carbon flow from root to the soil: root border cells (A), root hairs (B), and (C). The diagram on the right shows the main pathways of the nitrogen cycle. The green triangle denotes the processes that require labile carbon.

Figure 2. Exponential fit ($N_2O = 1.8_{1.5}^{2.2}*exp(1.8_{1.5}^{2.3} * \text{Tree growth rate}); R^2=0.7, n=33$) between monthly tree growth rates MgC ha$^{-1}$ month$^{-1}$ and soil N$_2$O fluxes from the km 67 eddy covariance tower site at the Tapajos National Forest, south of Santarem, Brazil. Monthly tree growth rates were obtained from dendrometry measurements on 1000 trees in four 4ha transects. Monthly soil N$_2$O fluxes were the geometric mean of 16 soil gas fluxes (two sampling dates, eight chambers each) from a 1 ha plot at the confluence of the transects.

Figure 3. Exponential relationship between overall forest growth rate (FGR) and a) wet season and b) annual soil N$_2$O flux in the Amazon basin. The symbols denote the different regions: triangles = Tapajos National Forest, circles = Caxiuana national Forest, and squares= Manaus. Exponential fits to the data resulted in N$_2$O flux = $0.7_{0.3}^{1.3} x \text{EXP}(\text{FGR} * 1.7_{1.5}^{1.9}), P<0.0001, R^2 = 0.9, n=14$, for the wet season data and N$_2$O flux = $2.8\pm1.0 x \text{EXP}(\text{FGR} * 0.97\pm0.12), P<0.001, R^2 = 0.97, n=6$. Although an exponential curve
was the best fit to the data at hand, we expect that at higher tree wood growth rates soil N$_2$O fluxes reach a plateau when carbon is not limiting microorganisms, or potentially decrease when very fast growth increases tree competition for nutrients and limit the microbial activity.

Figure 4. Predicted Amazon basin wide forest soil N$_2$O fluxes, based on the RainFor plot database and our exponential fit between soil N$_2$O flux and forest tree growth rate. Color of dots indicates N$_2$O flux in kg-N ha$^{-2}$ y$^{-1}$; colors ranges are: blue 0.4-2.0, green, 2.0-2.5, yellow 2.5-3.2, oker 3.2-3.8, and red 3.8-12.6 kg-N ha$^{-2}$ y$^{-1}$. Note that predicted N$_2$O fluxes are highest in the western Amazon basin, the area where no wet season or annual soil N$_2$O flux measurements ever have been collected.
Figure 1

C as CO₂ fixed in the leaves

Leaf drop

Phloem transport

Litter decomposition

N-cycling

Labile carbon intensive

Denitrification

N₂O

N₂

NO

NH₃

NO₂

NO₃

Organic N

NH₂

Ammonification/Mineralization

DNRA

Nitrification

Nitrifier denitrification

Biological fixation/immobilization

N-fixation

Labile carbon intensive

NH₄⁺

Nitrification

Phloem transport

C as CO₂ fixed in the leaves

Leaf drop

Litter decomposition
Figure 2

\[ y = 8.6016e^{1.4839x} \]

\[ R^2 = 0.7022 \]

- **2001**
- **2002**
- **2003**
- **2004**

Tree growth rate (mm mo\(^{-1}\))

**N\(_2\)O** (g-N m\(^{-2}\) h\(^{-1}\))

Tree growth rate (g-C ha\(^{-1}\) d\(^{-1}\))

- **★ 2001**
- **☐ 2002**
- **▲ 2003**
- **● 2004**
Figure 3

Mean wet season \( N_2O \) flux (\( g\cdot N\cdot m^{-2}\cdot h^{-1} \))

Mean annual \( N_2O \) flux (\( g\cdot N\cdot m^{-2}\cdot h^{-1} \))

Annual tree growth rate (\( MgC\cdot ha^{-1}\cdot y^{-1} \))
Figure 4
Supplemental Methods and Figures

We used Structural Equation Modeling (SEM) to determine the relative strength of the predictor variables on soil N\textsubscript{2}O fluxes, based on the overall covariation pattern of group of continuous variables. SEM is based on the a-priori development of one or several models rooted in cause-and-effect relationships, which then can be tested with statistically robust measures, such as the Basian Information Criterion (BIC). SEM modeling can both be used as a confirmatory and exploratory tool, though in the latter mode, only multiple a-priori models or the inclusion of certain a-priori variables can be tested\textsuperscript{2}. We used the polycor and SEM packages in R to analyze our data, both are described by Fox\textsuperscript{3}. Our model was loosely based our model development for the path analysis on Fritts\textsuperscript{4}, using the measured climatic variables at our tower site and the local tree growth rates from dendrometry measurements and monthly soil N\textsubscript{2}O fluxes (Figure 1). In short the model presumes that clouds and precipitation are the main drivers for both the recharging of soil water content (%WFPS) and incoming radiation (light). Light influences the air temperature, which influences the soil temperature, which in turn influences the soil microbial kinetics, and photosynthesis and thus tree growth rate. Tree growth rate is also affected by the air temperature through respiration. %WFPS influences the tree growth rate, because low moisture content will increase the water stress in the leaves and thus reduce the amount of water that will transported down the stem as phloem, which carries the carbohydrates used for stem growth. %WFPS, though oxygen limitation also influences the soil N\textsubscript{2}O production. Tree growth
presumably does this through nutrient supply as carbon and nitrogen substrate in litter
deposition, but also more directly through root exudation, which is the terminal end (for
the plant) of the phloem stream. The strongest path between precipitation and soil \( \text{N}_2\text{O} \) fluxes in the model was through either WFPS and tree growth rate or through light, air
temperature, and tree growth rate (Figure 2). Only when we excluded the link between
soil temperature and \( \text{N}_2\text{O} \) flux was the direct path between WFPS and soil \( \text{N}_2\text{O} \) flux
significant, though tree growth rate remained the strongest path (Figure 2b).

\textit{Process based models}

We acquired both the ForestDNDCTropica and PnET-DNDC model to determine
how these models predicted the overall ecosystem properties of the Tapajos site. We
then calibrated the PnET-DNDC model to the Tapajos National Forest site by extracting
site-based data for photosynthesis, respiration, and soil characterization from the
literature. We then modified the model parameters to optimize model outputs with the
existing Eddy-covariance tower, plot demography, phenology, soil moisture, and soil gas
flux data from the site in the Tapajos National Forest. We ran the model for ten years
with the same climate drivers (mean of the four years modeled) to ‘spin-up’ the model.
After the ten years we ran the four years (2001-2004) in continuous fashion.
References


Figure captions

Figure 1. Depiction of our simple model for the influence of environmental parameters and tree growth on soil N₂O fluxes. The terms along the arrows indicate the driver/process behind the influence of the predictor variable on the response variable.

Figure 2. Structural Equation Model (SEM) analysis based on our monthly dataset from the Tapajos National Forest in Brazil supports that tree wood growth is a strong predictor for soil N₂O fluxes. The size of the arrows depicts the strength of the relationship, with the values indicating the unstandardized coefficients (slope of the relationship\(^5\)) and the superscript denotes the statistical significance of the path.
Model for Temporal Soil Gas Fluxes

- Precipitation
- Light
- Air T
- Soil T
- %WFPS
- N₂O flux
- Clouds
- Photosynthesis
- Respiration
- Conductive heating
- Recharge
- Denitrification
- Phloem carbon transport
- Labile carbon
- Evaporation
- Microbial activity
- Radiation
- Tree GR
- Conductive heating
Model for Temporal Soil Gas Fluxes

Model Chisquare = 20.6  Df = 10 Pr(>Chisq) = 0.024
Chisquare (null model) = 259.45  Df = 21
Adjusted goodness-of-fit index = 0.85
RMSEA index = 0.18 90% CI: (0.06, 0.29)
Bentler-Bonnett NFI = 0.92
Tucker-Lewis NNFI = 0.91
Bentler CFI = 0.96
SRMR = 0.05
BIC = -14.3

Model Chisquare = 22  Df = 11 Pr(>Chisq) = 0.025
Chisquare (null model) = 259.45  Df = 21
Goodness-of-fit index = 0.84
Adjusted goodness-of-fit index = 0.59
RMSEA index = 0.18 90% CI: (0.06, 0.28)
Bentler-Bonnett NFI = 0.92
Tucker-Lewis NNFI = 0.91
Bentler CFI = 0.95
SRMR = 0.06
BIC = -16.5