Final Scientific/Technical Report
DE-SC0012416

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Title: Modeling the temporal dynamics of nonstructural carbohydrate pools in forest trees

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Project Period: 08/15/2014 - 08/14/2017

Report Submission Date: 11/09/2017

Executive Summary

Trees store carbohydrates, in the form of sugars and starch, as reserves to be used to power both future growth as well as to support day-to-day metabolic functions. These reserves are particularly important in the context of how trees cope with disturbance and stress—for example, as related to pest outbreaks, wind or ice damage, and extreme climate events. In this project, we measured the size of carbon reserves in forest trees, and determined how quickly these reserves are used and replaced—i.e., their “turnover time”. Our work was conducted at Harvard Forest, a temperate deciduous forest in central Massachusetts. Through field sampling, laboratory-based chemical analyses, and allometric modeling, we scaled these measurements up to whole-tree NSC budgets. We used these data to test and improve computer simulation models of carbon flow through forest ecosystems. Our modeling focused on the mathematical representation of these stored carbon reserves, and we examined the sensitivity of model performance to different model structures. This project contributes to DOE’s goal to improve next-generation models of the earth system, and to understand the impacts of climate change on terrestrial ecosystems.

Project Activities

Overview

Recent studies show that in mature forest trees, the nonstructural carbon (NSC) pool is surprisingly large, highly dynamic, and unexpectedly old. NSC reserves (mostly low molecular weight sugars and starch) play a vital role in carbon (C) allocation dynamics, and support metabolism throughout the year—most importantly when demand exceeds what is being concurrently supplied by photosynthesis.

Improved understanding of NSC allocation and consumption is crucial for predicting how trees may respond to global change and both biotic and abiotic stress factors. Yet, large knowledge gaps exist regarding the size, turnover, and seasonal dynamic of NSC pools.

Additionally there are uncertainties regarding optimal representation of allocation and storage processes in process-based simulation models of trees and forest ecosystems. This results in uncertainty of future projections of forest responses to climate change, and of the terrestrial C sink.

Objectives and Tasks

In this project, our main objective has been to construct detailed budgets of the size, age, and temporal dynamics of the NSC pool in forest trees in New England, and then to use these data to test and improve the representation of allocation and storage processes in computer simulation models.

Our motivating hypothesis is that proper representation of NSC pool dynamics is essential to model the capacity of forest ecosystems to tolerate biotic and abiotic stress factors, and is needed to improve forecasts of forest responses to climate change. Our modeling aims to provide new insights into both the physiology of C allocation processes and the role of NSCs in ecosystem C cycling. This has implications for the feedbacks of terrestrial ecosystems to atmospheric CO_2 and future climate.

Our project merges field studies at Harvard Forest (a mixed temperate forest in central New England) with ecosystem simulation modeling. Our objectives are:

- to construct whole-tree NSC budgets, and to determine how these vary over time and among species
- to estimate the mean age of soluble C using radiocarbon (^{14}C) methods, and to use this is a proxy for the mean residence time of stored NSC
- to use the above data to challenge various model representations of NSC reserves, and to investigate how ecosystem C cycling dynamics vary according to model structure

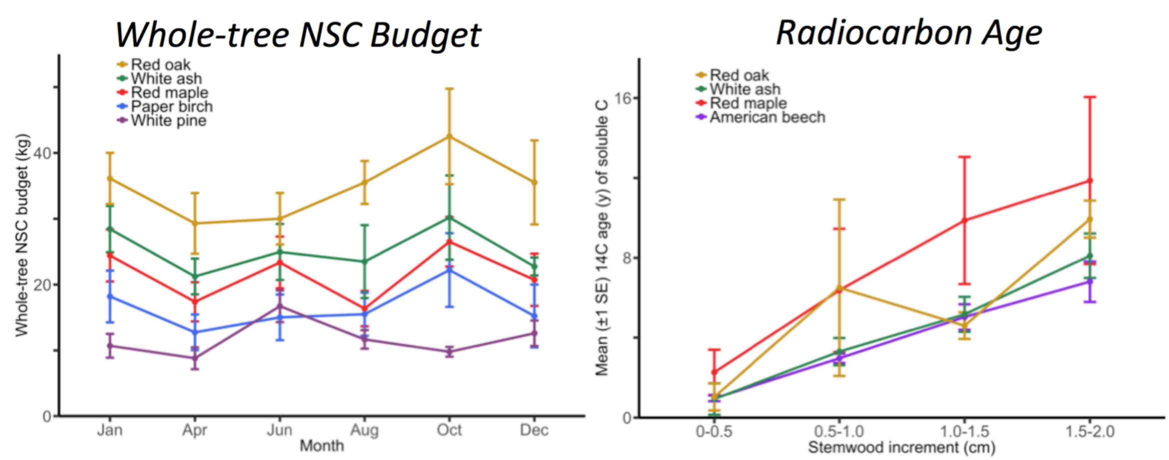
NSC Dynamics and Age

We completed field sampling to quantify seasonal variation in whole-tree NSC budgets at Harvard Forest. Briefly, we selected 24 trees for study, from red oak (*Quercus rubra*), white pine (*Pinus strobus*), red maple (*Acer rubrum*), paper birch (*Betula papyrifera*), and white ash (*Fraxinus americana*). Every month, for 12 months, we collected stem and root increment cores, as well as branch and foliage samples, from each tree. We accessed the upper canopy using a bucket lift. In the lab, we analyzed dried and ground samples to determine tissue concentrations of bulk sugars and starch. Additional samples were collected for radiocarbon analysis of soluble C compounds, to determine the age of stored sugars using the "^{14}C bomb spike" method, with AMS (accelerator mass spectrometry) analysis conducted at the University of California–Irvine. This work was led by Harvard PhD student Morgan Furze, who was supported by other funds (NSF fellowship and Harvard OEB Departmental support). A manuscript is in preparation.

At the whole-tree level, we found that NSC reserves are drawn down over the dormant season and built up over the growing season (Figure 1, left). However, different seasonal patterns are observed at the organ (root, stem, branch) level, implying a role for within-tree translocation of reserves. Seasonal patterns are also different for sugars (peak in winter) and starch (peak in autumn), implying different functional roles.

The age of extracted soluble C (Figure 1, right) increased with the age of the ring from which it is extracted, showing how 14C can be used as a tracer to distinguish "older" from "recent" photosynthate. Our data support the hypothesis of limited mixing of "new" photosynthates into "old" storage reserves. But, our hot-water extraction appears to pull out other soluble C compounds in addition to sugar (although sugar typically accounts for 50% or more of what is extracted). We are working on developing improved methods to purify sugar extracts, in collaboration with Andreas Richter at the University of Vienna.

Figure 1. Whole-tree NSC budgets (Left), and radial patterns of the radiocarbon age of soluble C (predominantly sugars) (right), for 5 temperate species growing at Harvard Forest.



Modeling

We used our new measurements to test and improve the model representation of NSC reserve dynamics. We focused on incorporation of progressively more complex representations of C allocation and NSC storage pools (e.g. Figure 2), and we investigated the consequences of different model representations for model performance and C cycle dynamics. This work was led by Veronika Ceballos-Nunez, a visiting PhD student from the Max Planck Institute in Jena Germany, and Harvard postdoc Tim Rademacher.

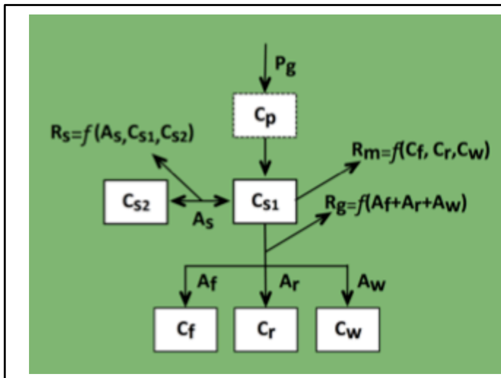
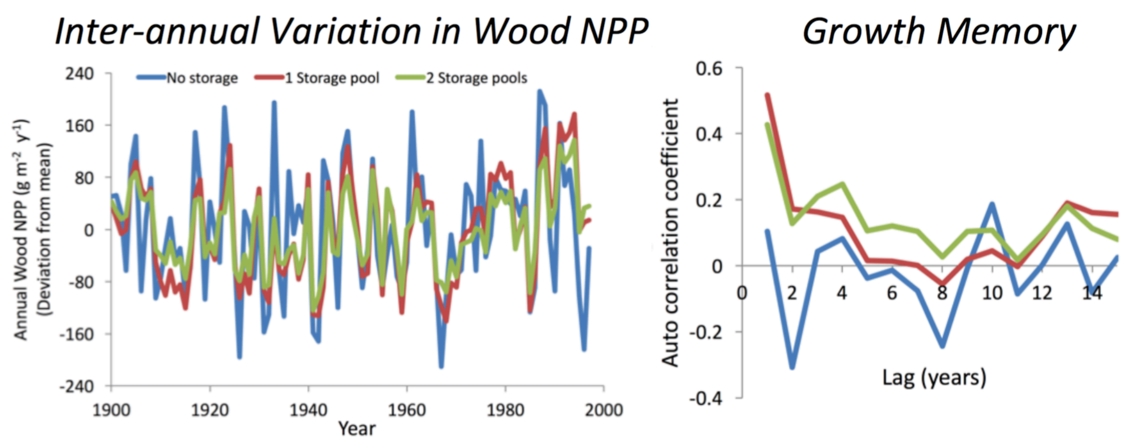


Figure 2. Example of "two pool" ("fast" and "slow" pools, for short and long-term storage) model representation of stored NSC reserves.

Ceballos-Nunez conducted an analysis using the age of C in different pools, and the overall transit time of C through the system, as diagnostics to assess how different carbon allocation schemes influence rates of C cycling. Interestingly, the different model structures did not influence how much C was stored in the system at the conclusion of the model run, but they did result in large differences in age and transit time distributions. The inclusion of two storage compartments resulted in the prediction of a system mean age that was 7-10 years older than in the models with one or no storage compartments. As expected from these age distributions, the mean transit time for the model with two storage compartments was longer than for the other two models. These results suggest that ages and transit times, which can be indirectly measured using isotope tracers (e.g. our ^{14}C measurements), serve as important diagnostics of model structure and could largely help to reduce uncertainties in model predictions. A manuscript based on this work has undergone peer review at *Biogeosciences*, and is currently in revision for publication in that journal.

Rademacher developed different representations of NSC storage for inclusion in the ecosystem model, PnET and investigated how model structures influenced interannual variation in wood NPP. Our ^{14}C data were used to constrain NSC mean residence times. In a 300-year simulation run for Harvard Forest, interannual variation in wood NPP was almost twice as large for the no-pool run as the two-pool run, indicating a greater sensitivity to environmental variation (Figure 3, left). Autocorrelation of wood NPP, a measure of growth "memory", was stronger for models that included storage, but did not persist much beyond a 1 year lag (Figure 3, right). This is weaker than observed in tree-ring based studies, suggesting potential for further model improvement. Rademacher continues to conduct analyses to investigate how stored reserves increase resilience to stress factors including defoliation, drought, and extreme weather. This work is expected to lead to a publication.

Figure 3. Influence of model representation of NSC storage on the dynamics of annual wood NPP (left), and growth memory as measured by the autocorrelation coefficient (right).



Conclusions

Trees store large amounts of NSC in the form of sugars and starch. These reserves vary dynamically over the course of the year, but ^{14}C data show that they can be retained for many years. Model-based analyses indicate that these reserves serve to reduce the impact of weather on year-to-year variation in tree growth, but that the way in which C allocation processes are represented in the model has an influence on ecosystem C dynamics, including C transit times. Future work will investigate the role of NSC in mediating responses to biotic and abiotic stress factors. This work highlights the importance of realistic modeling of NSC reserves in the context of tree growth and the terrestrial C sink.

<u>Products developed under the award</u>

a. Publications:

Ceballos-Nunez, V., A.D. Richardson and C.A. Sierra. 2018. Ages and transit times as important diagnostics of model performance for predicting carbon dynamics in terrestrial vegetation models. *Biogeosciences*, in revision.

b. Web sites: None.

c. Networks or collaborations fostered: New collaborations were developed with researchers from the Max Planck Institute for Biogeochemistry, Jena Germany, and the Department of Chemical Ecology and Ecosystem Research, University of Vienna, Vienna Austria.

d. Technologies/Techniques: none.

e. Inventions/Patent applications: none.

f. Other products:

Conference and workshop presentations:

- Furze, M., T. Rademacher, and A.D. Richardson. 2017. Measuring and modeling the size and temporal dynamics of nonstructural carbon reserves in temperate forest trees. Poster presented at the DOE ESS PI Meeting, Bolger Center, Potomac MD, 25-26 April 2017.
- Furze, M., B. Huggett, C. Stolz, D. Aubrecht, M. Carbone and A.D. Richardson. 2015. Quantifying the size and temporal dynamics of nonstructural carbon in temperate forest trees. Poster presented at the 26th Harvard Forest Ecology Symposium, Petersham MA, 17 March 2015.
- Furze, M., B. Huggett, C. Stolz, D. Aubrecht, M. Carbone and A.D. Richardson. 2015. Quantifying the size and temporal dynamics of nonstructural carbon in temperate forest trees. Poster presented at the DOE ESS PI Meeting, Bolger Center, Potomac MD, 28-29 April 2015.

In 2015, 2016, and 2017, PI Richardson also served as co-convener for oral and poster sessions related to this project ("Carbon allocation in plants and ecosystems: mechanisms, responses and biogeochemical implications") at the European Geosciences Union annual meeting in Vienna, Austria. These sessions were extremely well subscribed, and generated enthusiastic response within the community.

Seminars

Richardson gave seven seminar/colloquia presentations related to this project:

- Northern Arizona University, College of Engineering, Forestry and Natural Sciences, Flagstaff AZ, May 2016.
- Indiana University, Ecology, Evolution and Behavior Seminar Series, Bloomington IN, April 2016
- Cornell University, Biogeosciences Seminar Series, Ithaca, NY, April 2015.
- University of Pennsylvania, Department of Biology, Philadelphia, PA, April 2015.

- Harvard University, Harvard University Herbaria, Cambridge, MA, March 2015.
- Harvard University, Harvard Forest, Petersham MA, March 2015.
- Lund University, Department of Physical Geography and Ecosystem Sciences, Lund, Sweden, November 2014.