

Probability distributions of non-structural carbon ages and transit times provide insights in carbon allocation dynamics of mature trees

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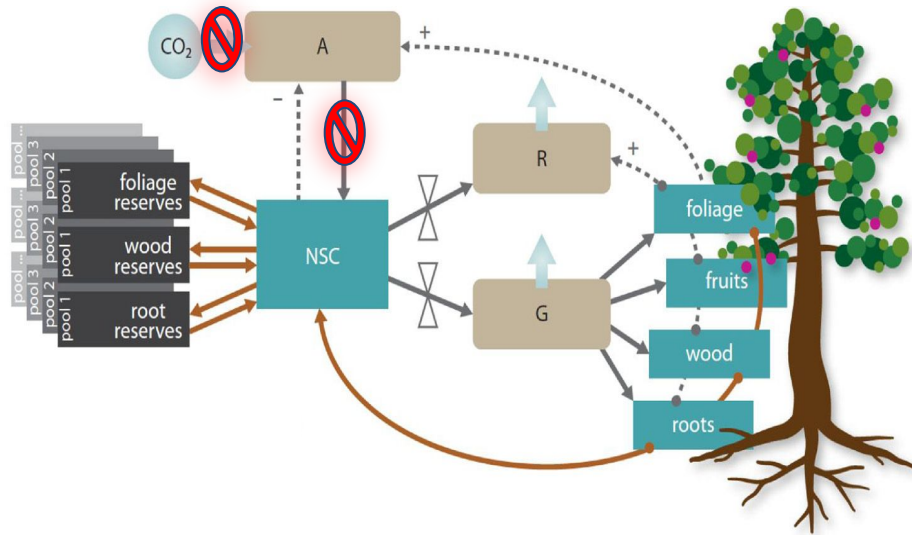
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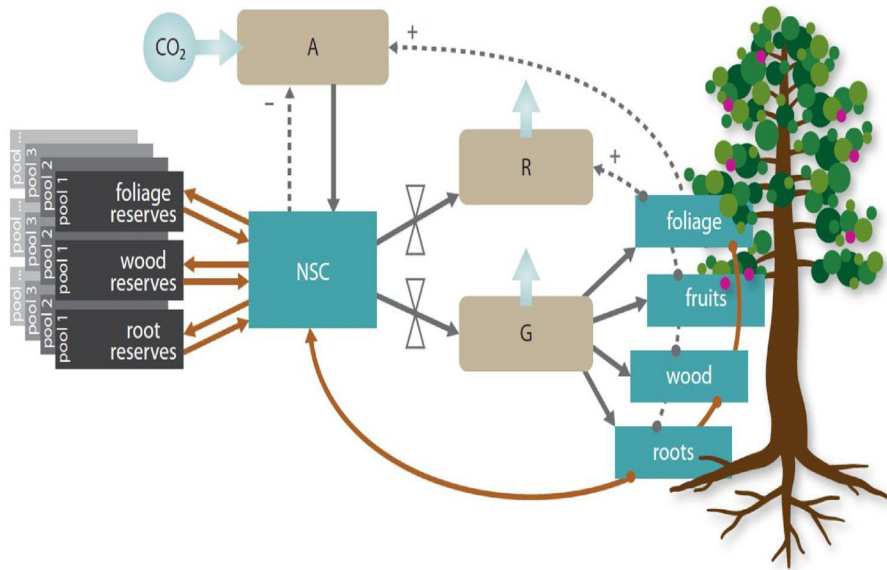
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Introduction



When carbon assimilation is limited in trees, the availability and mobility of the non-structural carbon reserves (NSC), mostly sugar and starch, supports trees' metabolism and growth and increases trees' ability to survive stressful conditions.

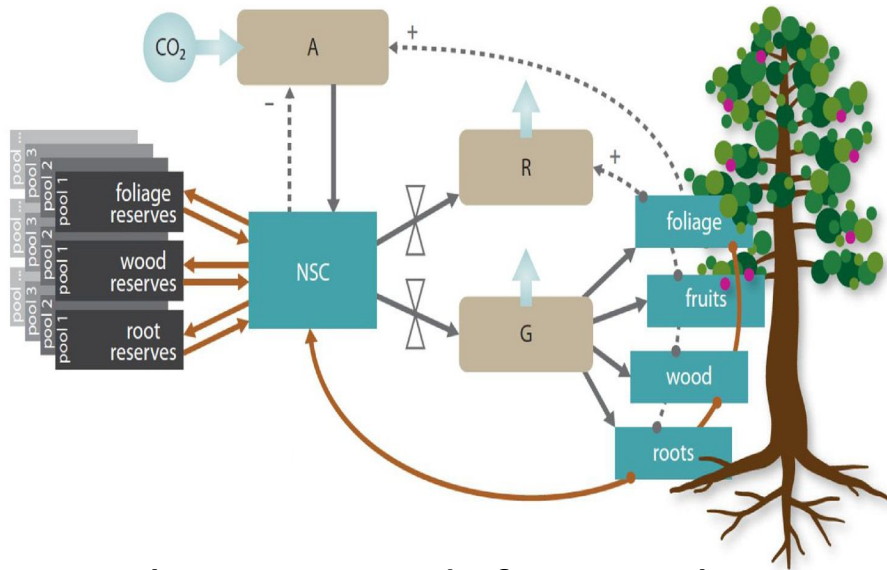
Introduction



This NSC availability and mobility is part of the carbon allocation process which is described by the model in the figure, where each arrow represents a carbon flux and each box a carbon pool.

Here, there are several pools for NSC, one transient NSC pool (NSC blue box) and several stored NSC called reserves (black boxes).

Introduction

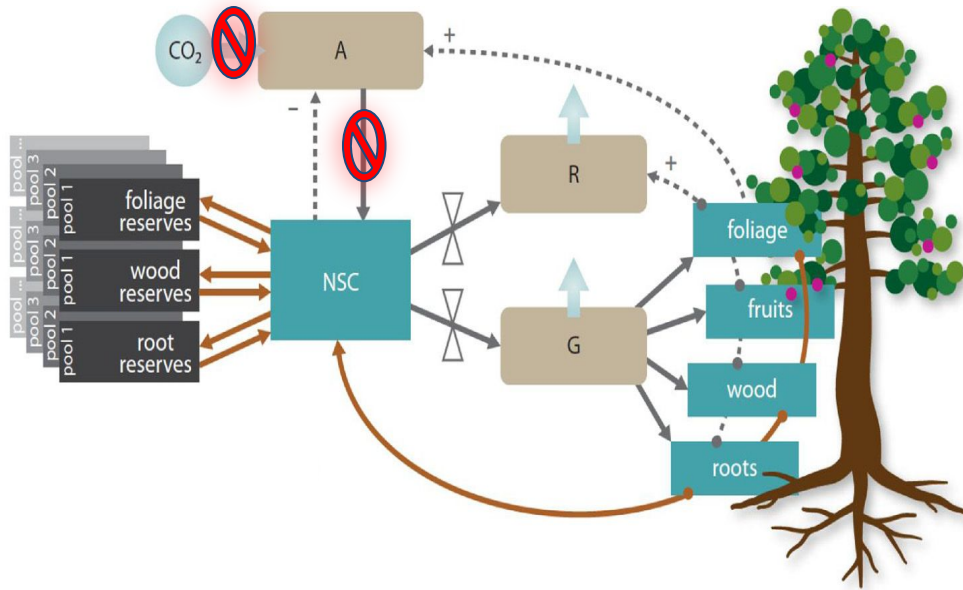


The dynamics of the C between the different C pools in a tree will determine the C age and C transit time for each C pool and for the entire tree.

Carbon age is defined as the time elapsed since the C was fixed until a moment of observation, for our tree in the model it is the age of the carbon inside the tree since it was fixed.

Carbon transit time is defined as the time between C is fixed until it leaves the system, in this case it is until C is respired or lost in litter fall (light blue arrows out of R and G pools in the figure).

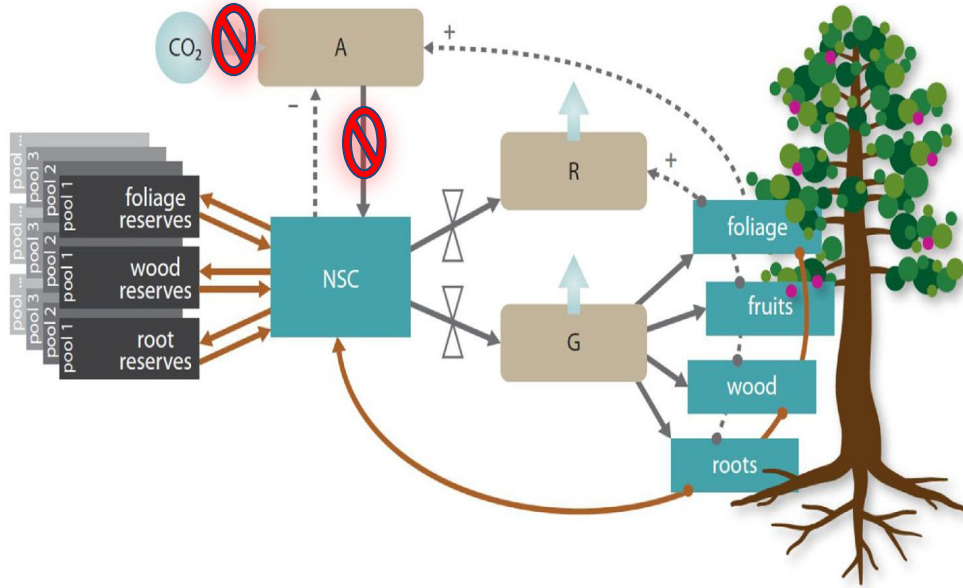
Introduction



Differences in the carbon dynamics between trees will be reflected in the carbon ages and transit times distributions of the NSC.

Under outstanding carbon limitation, the changes in the age and transit time distribution would tell us what is the age structure of the NSC reserves that supports trees metabolism and how fast trees would consume those reserves.

Introduction



To date, we lack systematic understanding about how NSC age distributions differ between tree organs and tree species, and about the differences between species in the use of the NSC reserves under outstanding carbon limitations.

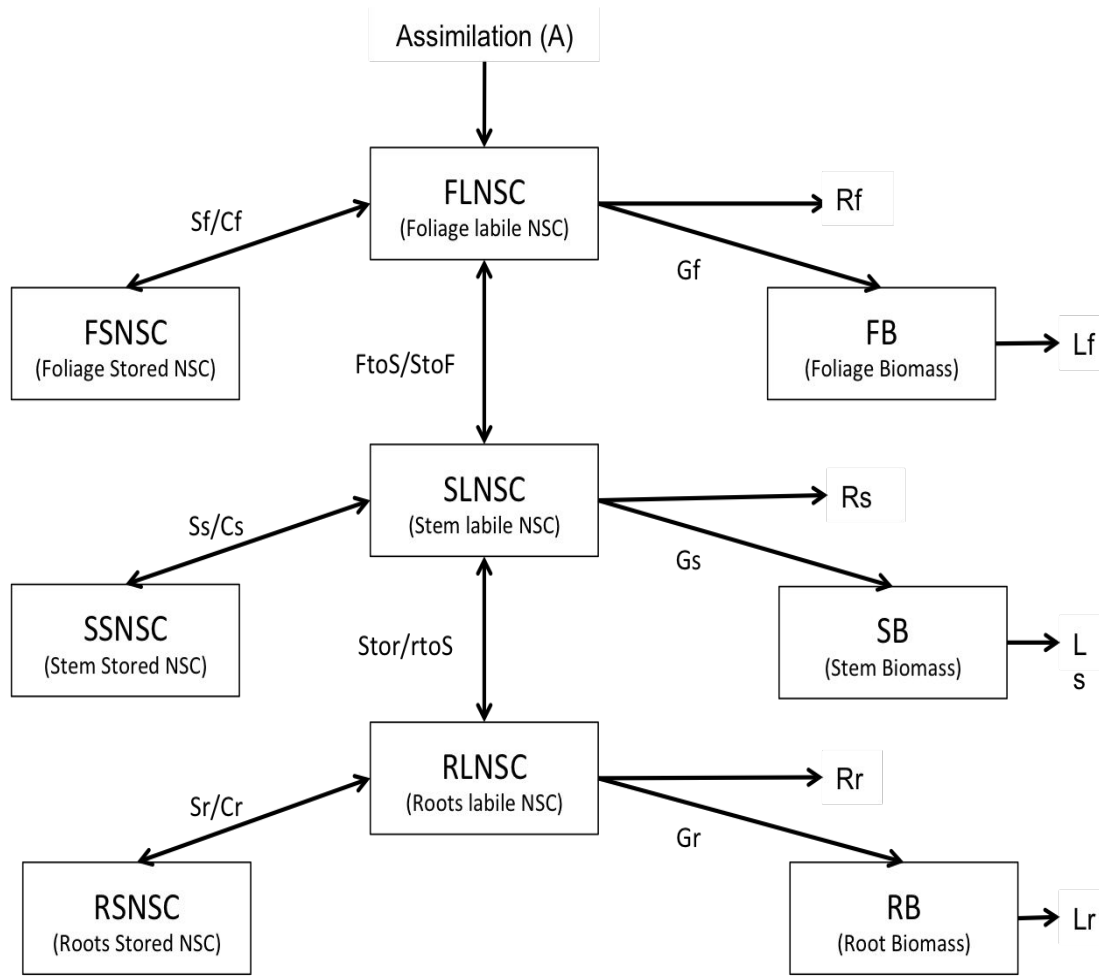
The representation of carbon allocation in compartmental systems allows estimations of NSC age and transit time distributions, and their changes under stressful conditions.

Questions

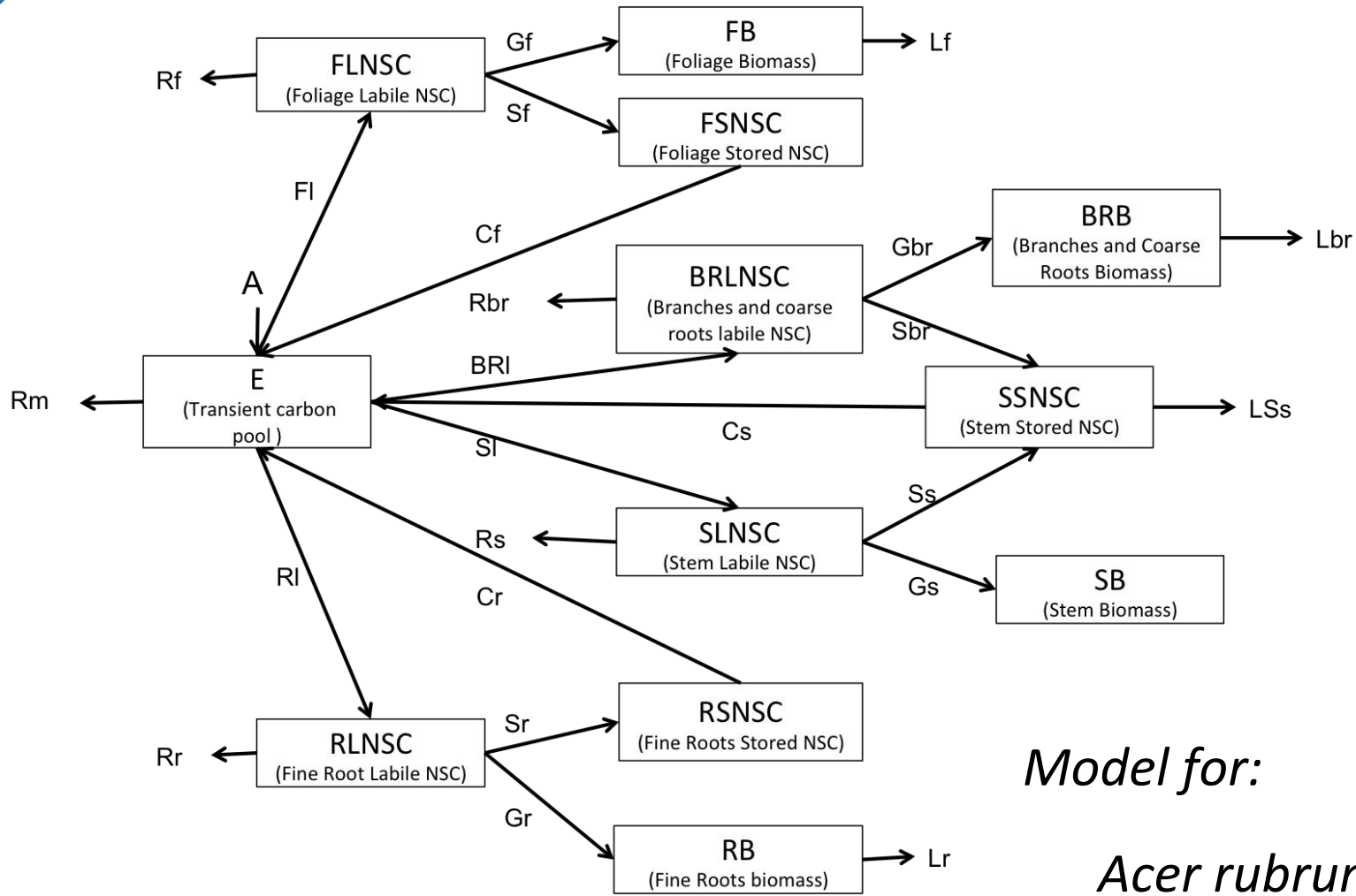
- i) How different are the predictions of NSC dynamics overall and between tree organs, for contrasting plant types (evergreen vs. deciduous) or for contrasting environmental conditions (severe growth limitations vs. favorable conditions)?
- ii) What is the predicted age structure of the NSC reserves available and how long, theoretically, trees would take to consume these reserves?
- iii) What are the principal carbon fluxes that influence the NSC mean ages and mean transit times?

Models

We used two parameterized carbon allocation models from the literature: the first one for *Pinus halepensis* proposed by Klain and Hoch (2015), and the second one for *Acer rubrum* and *Pinus taeda* proposed by Ogle and Pacala (2009) (next slide).



Models



Model for:

Acer rubrum

Pinus taeda

Ogle and Pacala 2009

Models

From these models we calculated the annual fraction of carbon that leaves each pool as the ratio of the flux divided by the pool size of the donor pool. These fractions were used as the model parameters for our calculations.

Models

$$\frac{d\vec{x}(t)}{dt} = \mathbf{B} \cdot \vec{x}(t) + \vec{\beta} \cdot u(t) \quad eq. 1$$

$$\mathbf{B} = \begin{bmatrix} a_{1,1} & a_{1,2} & a_{1,3} & \dots \\ a_{2,1} & a_{2,2} & a_{2,3} & \dots \\ a_{3,1} & a_{3,2} & a_{3,3} & \dots \\ \vdots & \vdots & \vdots & \ddots \end{bmatrix}$$

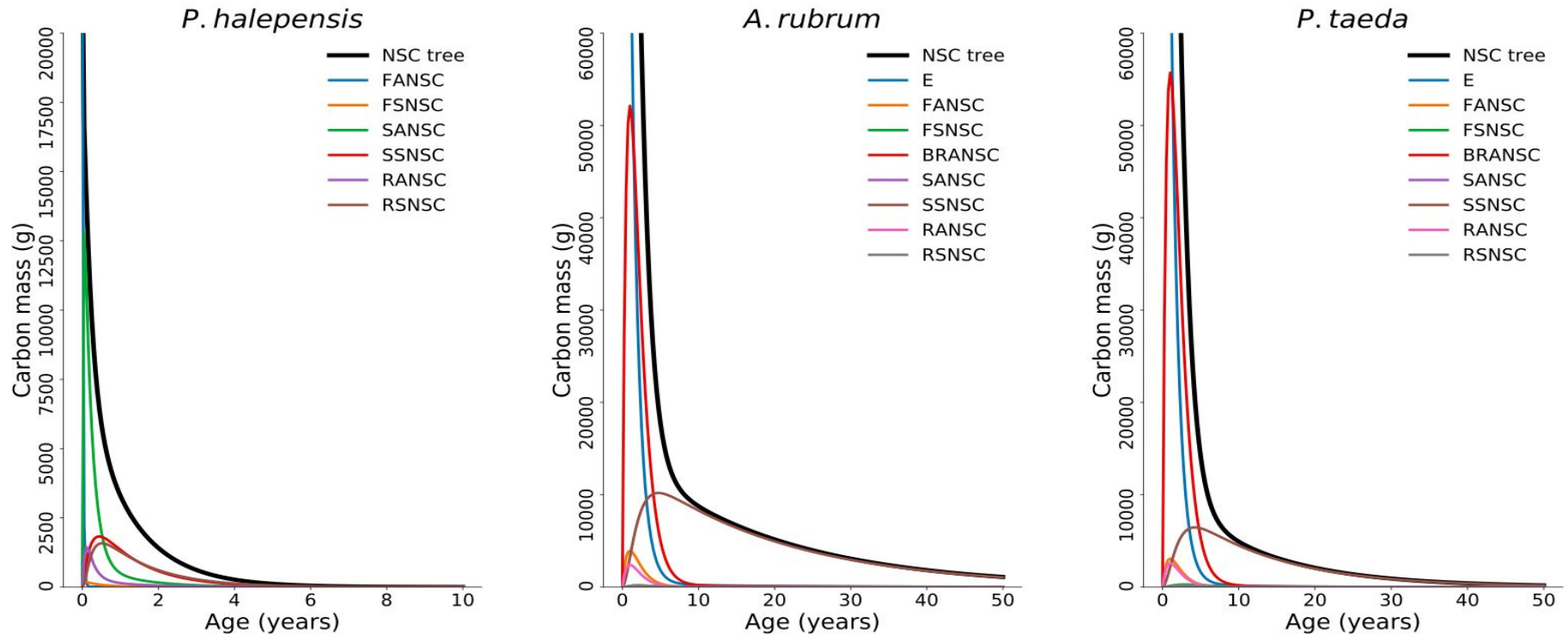
The models were described with a system of ordinary differential equations expressed in the general linear non-autonomous form (eq. 1). Here, B is a mxm square matrix where m is the number of compartments in the model, the diagonal elements are the fraction of carbon leaving each pool and the off-diagonal entries are the annual fraction of carbon transferred among compartments.

Models

$$\frac{d\vec{x}(t)}{dt} = \mathbf{B} \cdot \vec{x}(t) + \vec{\beta} \cdot u(t) \quad eq. 1$$

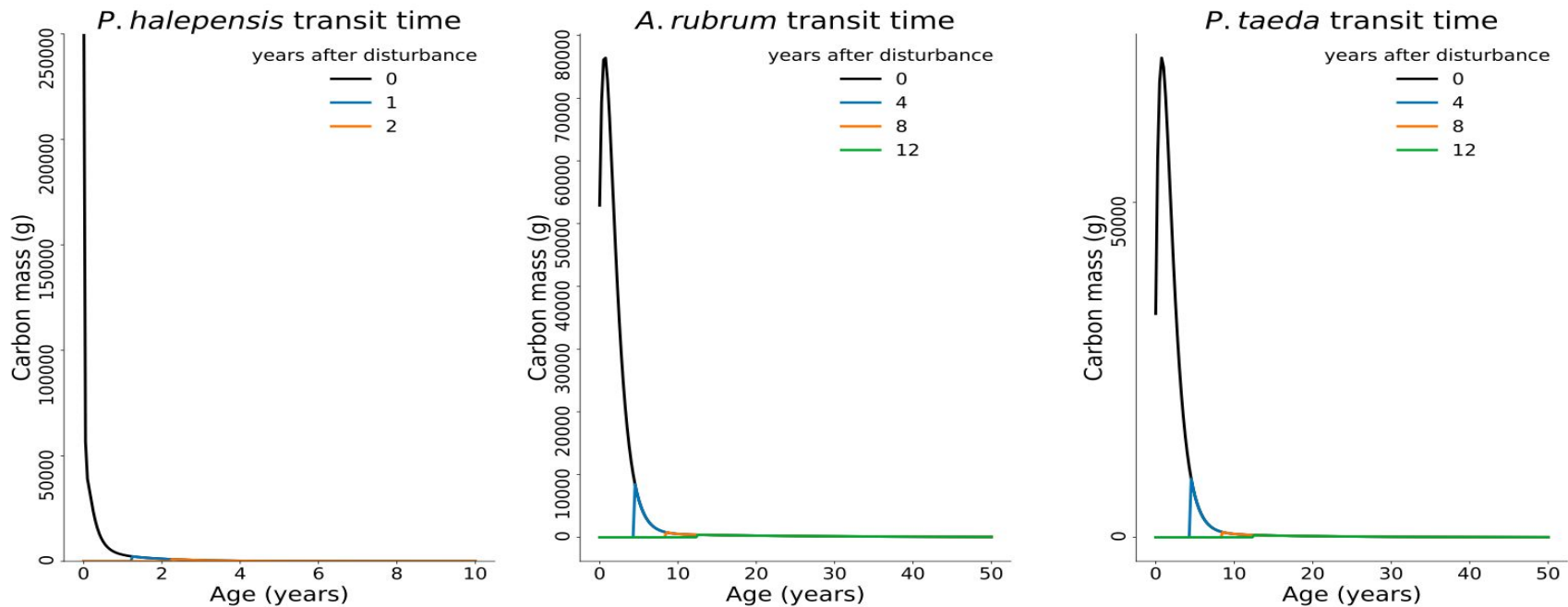
From this representation we used the formulas reported by Metzler and Sierra (2018) and Metzler et al., (2018) to estimate the age and transit time distributions of mature trees from our models in steady state, and to estimate the changes in these distributions when an outstanding carbon limitation scenario was simulated (out of steady state).

Results: age distributions



Age distribution of the non-structural carbon in the whole tree and the tree pools for each species *Pinus halepensis*, *Acer rubrum* and *Pinus taeda*. The frequencies are given in grams of carbon and the sum of all the frequencies of all the compartments is equal to the total mass of carbon of the system. This tell us how much carbon of an specific age can be found in a tree or a tree's organ.

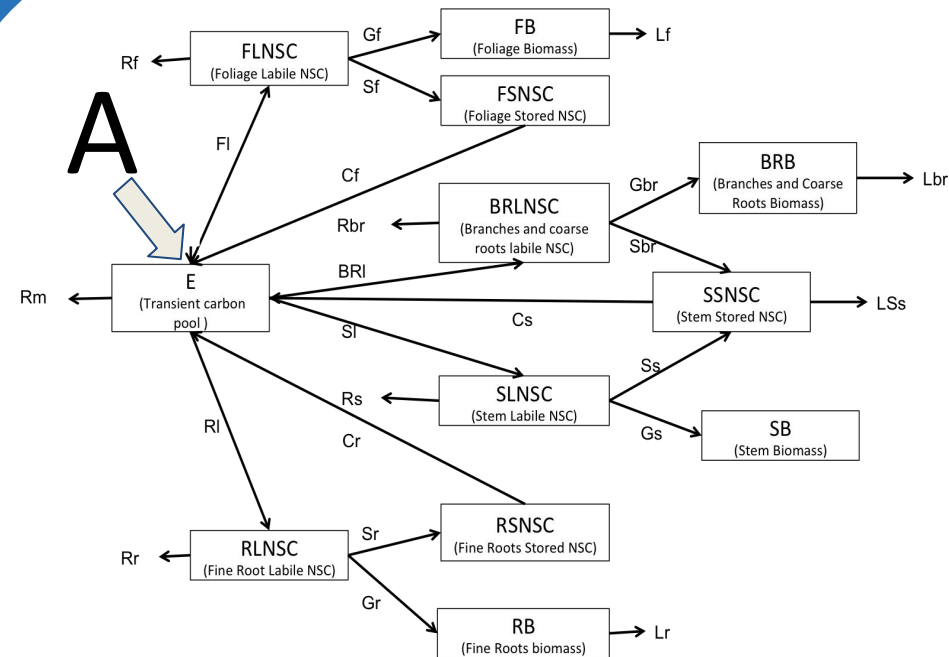
Results: system transit time distributions



Backward transit time distribution of the non-structural carbon in the whole tree during healthy conditions (Year 0 after disturbance) and years subsequent to the start of the simulated carbon limitation for each of the species *Pinus halepensis*, *Acer rubrum* and *Pinus taeda*.

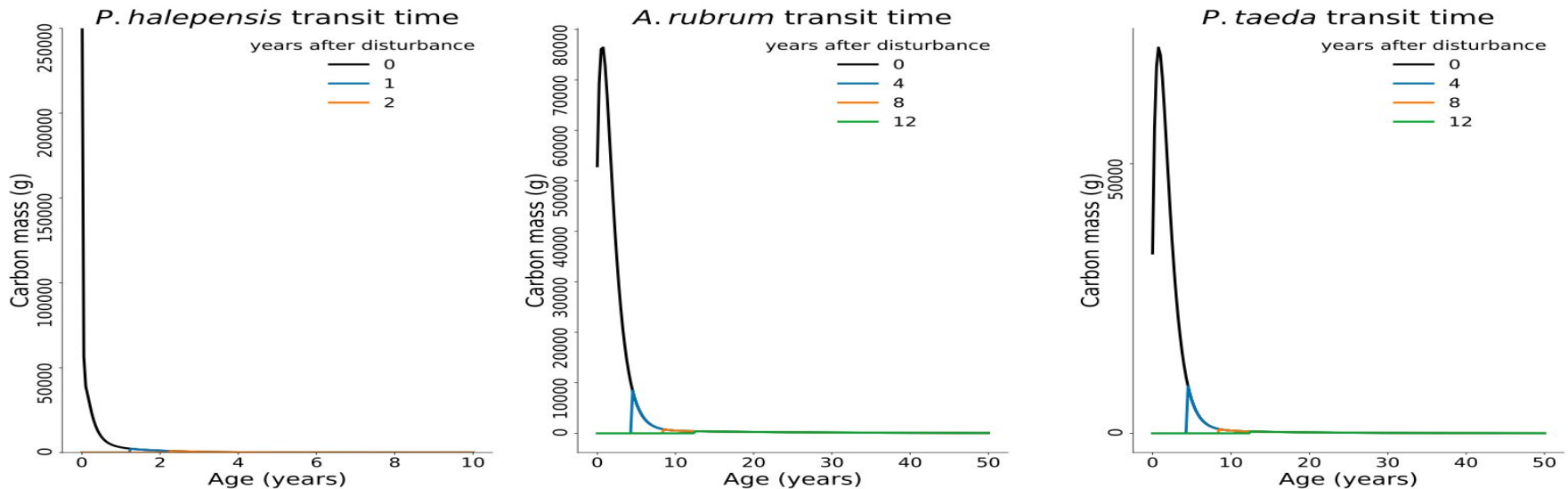
Here it is important to notice that most of the carbon that is respired when trees are healthy (black line) is mainly young, but when they get to starve it becomes older very quickly because trees start exhausting the NSC storage pool.

Results: system transit time



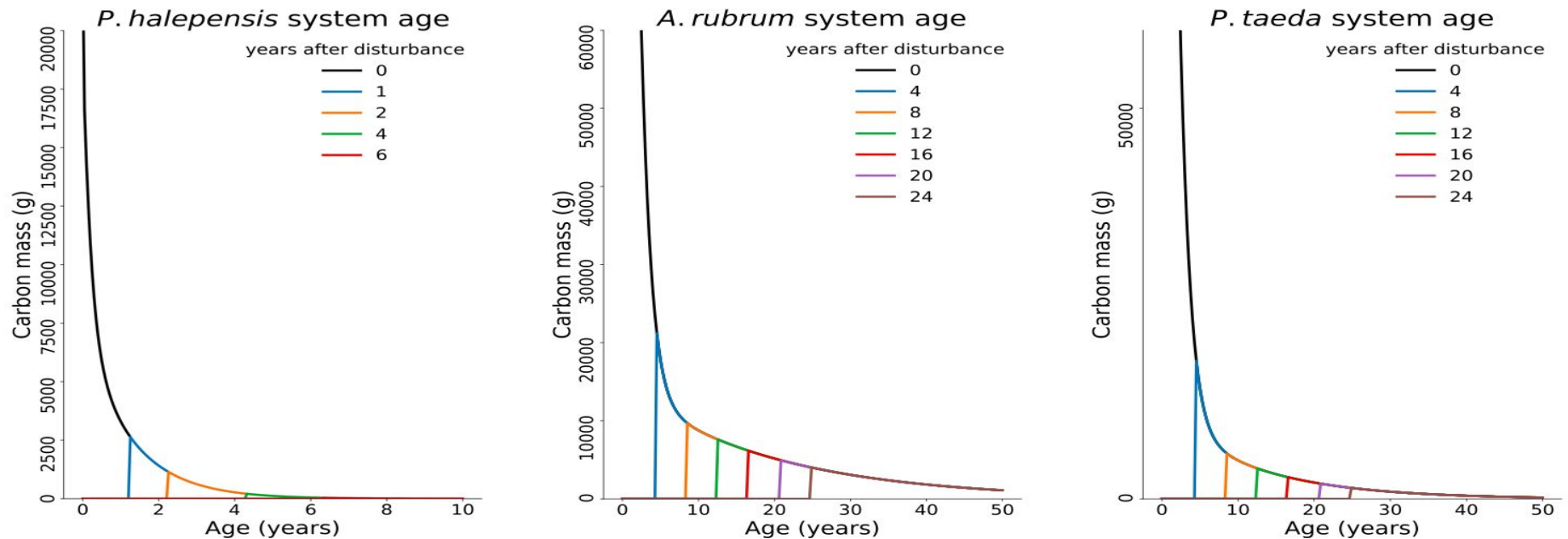
The NSC transit time distributions describe the age structure of the carbon that is being used (leaving the system) in metabolism and growth, and reflects the age structure of the main source of carbon. For healthy trees it is the recently assimilated carbon (A), when trees are stressed this distribution reflects the age structure of the stored carbon.

Results: system transit time



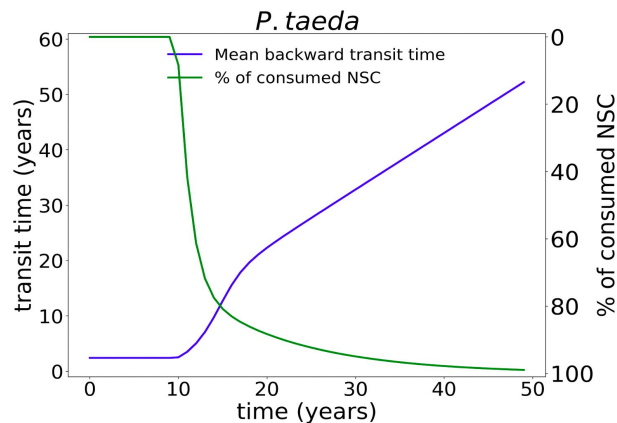
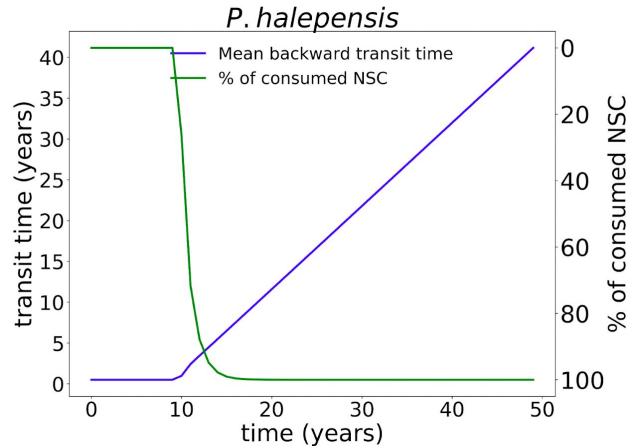
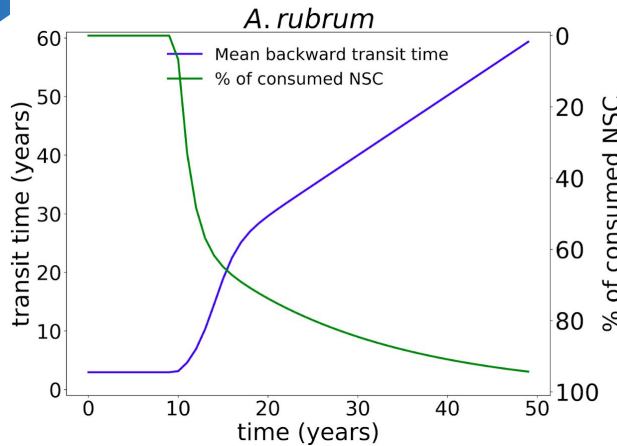
This progressive shift in the transit time from mainly young to older respired carbon has been already documented. It has been explained by the last in first out principle. Nevertheless here we provide an alternative: it can be explained by the distribution of the carbon ages, where in healthy individuals the young carbon is more abundant and in stressed individual this young carbon is exhausted quicker than the old carbon leading to an increase in the transit time, due to the higher probability of young carbon to be used

Results: system age



Age distribution of the non-structural carbon in the whole tree for years subsequent to the start of the carbon limitation simulation (years after disturbance) for each of the species *Pinus halepensis*, *Acer rubrum* and *Pinus taeda*. In the simulation the young carbon starts to diminish faster than the old carbon until approximating a uniform distribution.

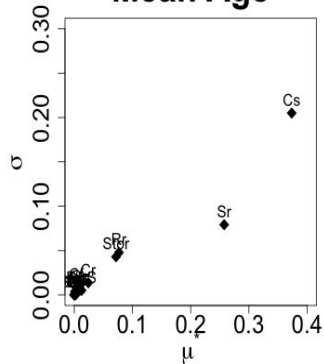
Tracking the transit time



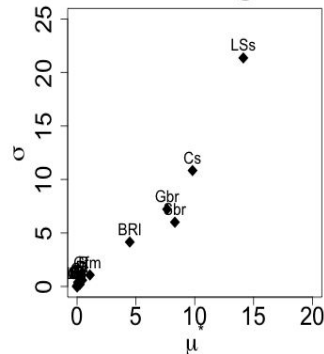
Non-structural carbon mean backward transit time and the percentage of NSC consumption during 50 years of the simulation for each species *Pinus halepensis*, *Acer rubrum* and *Pinus taeda*. The first 10 years of the simulation represent the steady state, with trees growing under healthy conditions. After this, assimilation was set to zero to simulate carbon limitation for the subsequent 40 years. For a given time step of the simulation there is a level of consumption given by the green line and specified in the right axis, and there is a backward transit time given by the blue line and noted in the left axis. This means backward transit time reflects the mean age of the carbohydrates being used in metabolism and growth in each time step of the simulations and we can track it under stressful conditions.

Results: sensitivity

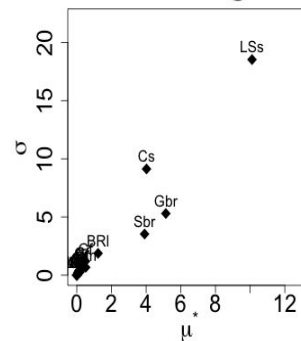
P. halepensis
Mean Age



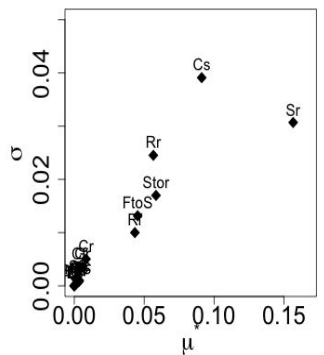
A. rubrum
Mean Age



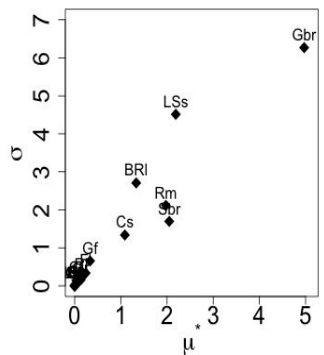
P. taeda
Mean Age



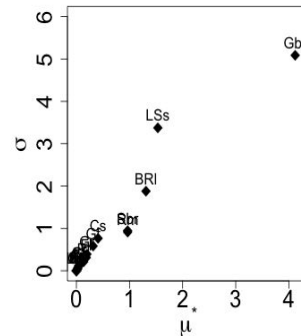
Mean Transit Time



Mean Transit Time



Mean Transit Time

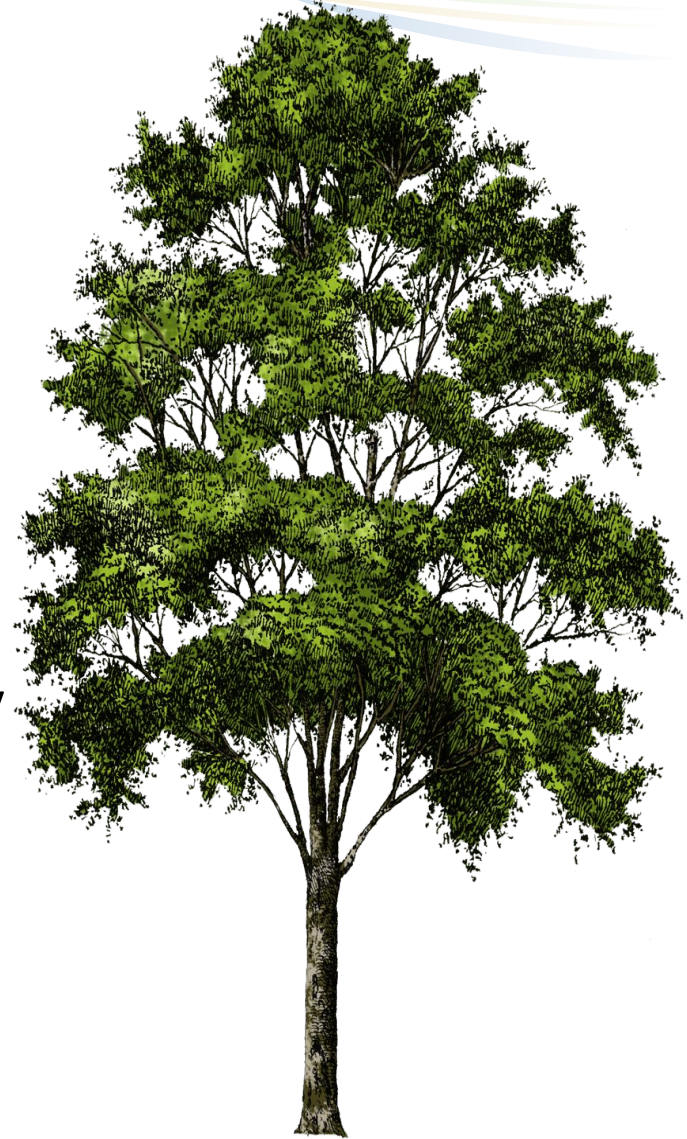


Mean sensitivity value μ and its correspondent variance σ for each flux of each species (*Pinus halepensis*, *Acer rubrum* and *Pinus taeda*) calculated by the Elementary Effects method.

The fluxes that had the biggest influence in the mean carbon age and mean transit time were the ones related with the use of stored NSC (LSs and Cs) in the wood and with root fluxes in general (Sr, Gbr, Rr, Brl).

In conclusion!

Our estimates are relevant for characterizing general differences in the NSC dynamics in contrasting tree species, identifying different storage traits based on plant type and growth environment; predicting how trees use their reserves under stress, e.g., the exponential-linear increase of the NSC transit time as trees exhaust their reserves; providing a plausible probabilistic interpretation about why trees consume primarily young carbon during healthy stages and why this shifts after a prolonged carbon limitation; and identifying the determinant sink fluxes in NSC dynamics for mature trees.



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Thank you!

Read the complete paper:

Herrera-Ramirez, D., Muhr, J., Hartmann, H., Römermann, C., Trumbore, S. E., Sierra, C. (2020). Probability distributions of non-structural carbon ages and transit times provide insights in carbon allocation dynamics of mature trees. New Phytologist. doi:[10.1111/nph.16461](https://doi.org/10.1111/nph.16461).



Thank you!

References:

Hartmann H, Adams HD, Hammond WM, Hoch G, Landh ausser SM, Wiley E, Zaehle S. 2018. Identifying differences in carbohydrate dynamics of seedlings and mature trees to improve carbon allocation in models for trees and forests. *Environmental and Experimental Botany* 152: 7–18.

Ogle K, Pacala SW. 2009. A modeling framework for inferring tree growth and allocation from physiological, morphological and allometric traits. *Tree Physiology* 29: 587–605.

Klein T, Hoch G. 2015. Tree carbon allocation dynamics determined using a carbon mass balance approach. *New Phytologist* 205: 147–159.