Non-structural carbon ages and transit times provide insights in carbon allocation dynamics of mature trees

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Total word count: 6725; Introduction: 1152; Materials and Methods: 2030; Results: 1282; Discussion: 1927; Limitations and conclusions 325; Number of figures: 8; Figures in color: 3, 4, 5, 6, 8; Number of tables: 4.

# Summary

* The trees’ use of non-structural carbon (NSC) to survive supply shortages impacts the age structure of the NSC. We compared model predictions of NSC ages and transit times for three tree species with different leaf phenology and growth environments *Pinus halepensis* Mill., *Acer rubrum* L. and *Pinus taeda* L. to understand differences in carbon storage dynamics.
* We used two carbon allocation models from the literature to estimate the NSC age and transit time distributions, to simulate assimilation shortage (“starvation”), and to evaluate the sensitivity of the mean ages to changes in allocation fluxes.
* Differences in allocation resulted in different NSC age and transit time distributions. The simulated starvation flattened the NSC age distribution and increased the mean NSC transit time, which can be used to estimate the age of the NSC available and the time it would take to exhaust the reserves. The outflow of the NSC stored in the wood and the root fluxes had the biggest impact on the mean NSC age and transit time.
* Our results showed how trees with different storage traits are expected to react differently to starvation. This vulnerability to starvation is evidenced in how NSC transit time and age distributions change.

**Keywords**  
Carbon allocation, non-structural carbohydrates, tree storage dynamics, carbon ages and transit times, tree carbon dynamics modeling.

# Introduction

The availability and mobility of the non-structural carbon (NSC) reserves, mostly sugars and starch, determine trees’ ability to survive photosynthetic shortages (Dietze *et al.*, 2014; Hartmann & Trumbore, 2016; Martínez-Vilalta *et al.*, 2016; Overdieck, 2016; Trugman *et al.*, 2018; Wiley *et al.*, 2019). Carbon limitation may happen because droughts, physical damage, pests, diseases, and floods, are becoming more frequent due to climatic changes (IPCC, 2018; Klein & Hartmann, 2018). Tree mortality associated with these stressful conditions (Bréda *et al.*, 2006; Carnicer *et al.*, 2011; von Arx *et al.*, 2017) may cause biodiversity loss (Nunez *et al.*, 2019), economic losses (Strand, 2017; Oliveira *et al.*, 2019) and long-term modifications to the global carbon cycle (McDowell *et al.*, 2018; Pugh *et al.*, 2019). Under stress, trees mobilize NSC from their storage reserves to sustain metabolic and growth requirements (Anderegg & Anderegg, 2013; Klein & Hoch, 2015; Mei *et al.*, 2015). Although carbon allocation has been widely investigated during the last decades, it is a complex process that still has not been fully understood mechanistically (Hartmann & Trumbore, 2016). In general, carbon fixed during photosynthesis is transported as NSC from chloroplasts to different plant organs (e.g., leaves, branches, stems, and roots) where it is allocated either to metabolism (respiration, growth, defense, osmotic regulation, among others) or to storage, which may occur passively or actively (Lacointe *et al.*, 2004; Wiley *et al.*, 2013; Huang *et al.*, 2019b). To understand these dynamics, compartmental models have been proposed where NSC is allocated in organ specific compartments (e.g., leaves, stems and roots) and compound specific compartments (e.g., active labile carbon and stored labile carbon), which are known to have different cycling dynamics (Richardson *et al.*, 2012; Klein & Hoch, 2015; Ceballos-Núñez *et al.*, 2018). The active labile carbon is quickly cycled through the tree and replenished mostly by the influx of newly assimilated carbon, resulting in an accumulation of mainly young ( year old) carbon in these pools (Gaudinski *et al.*, 2009; Carbone *et al.*, 2013; Richardson *et al.*, 2015). In contrast, the stored NSC, which has been represented mostly as a passive allocation pool, accumulates when photosynthesis surpasses demand and is retrieved at slow rates, resulting in an increase in the age of the carbon in these pools (Richardson *et al.*, 2015). These two compartments have been associated with specific compounds -sugar and starch- (Klein & Hoch, 2015), but reported similar ages in both compounds do not support this generalization (Richardson *et al.*, 2015). Despite recent efforts, it is still difficult to differentiate and measure fast and slow cycling pools of NSC in trees. Alternatively, Trumbore *et al.*, (2015) explained the differences in NSC dynamics in the stem-wood with a simple diffusion model of one NSC compartment with a radial mixing of carbon of different ages. The mixture of NSC inwards in the wood, along rays, is older with respect to the mixture of NSC in the outward direction because of the proximity to the carbon source-phloem. Above all, a proper detailed representation of carbon allocation in models may improve our ability to estimate and understand NSC dynamics.

NSC dynamics determine the ages of the carbon in the different organ specific and compound specific pools in trees and its transit time. Carbon age is defined as the time elapsed since a carbon atom enters the system until the time of observation (Bolin & Rodhe, 1973), i.e., age zero represents the moment of carbon fixation from the atmosphere. Transit time is defined as the time that a carbon atom remains in the system until it exits (Ceballos-Núñez *et al.*, 2018). To give an example: when defining our observed system as all the NSC in a tree, carbon atoms would enter through photosynthesis (with age equal to zero) and leave when being allocated to the formation of structural tissue (growth) or to catabolic requirements (i.e., loss as CO2). Here, we define NSC transit time as the time elapsed between these two points. These definitions allow us to estimate the distributions of the NSC ages and NSC transit times across all carbon pools using models, but the precise measurement of these quantities remains elusive (Ceballos-Núñez *et al.*, 2018; Metzler *et al.*, 2018). Nonetheless, the mean age and mean transit time of the NSC of different organs have been estimated from 14C measurements in the sugars and the respired 14CO2, respectively, and by pulse labeling techniques in trees (Carbone *et al.*, 2006, 2013; Epron *et al.*, 2012; Trumbore *et al.*, 2015; Muhr *et al.*, 2016, 2018). In particular, NSC allocated to respiration and growth under healthy conditions where carbon assimilation is not limited consists mainly of current year carbon ( year old) (Richardson *et al.*, 2015; Muhr *et al.*, 2018). However, previous studies have shown that trees start mobilizing stored carbon when carbon supply is limited, resulting in an increase in the age of the metabolized carbon (Vargas *et al.*, 2009; Carbone *et al.*, 2013; Trumbore *et al.*, 2015; Ceballos-Núñez *et al.*, 2018; Muhr *et al.*, 2018). The differences in the quantity and mobility of this stored carbon among different trees and/or between organs in the same tree may result in different NSC age distributions. To date, we lack systematic understanding about how different are the NSC age distributions between tree organs and tree species, and about the differences in the use of the NSC reserves under outstanding carbon source-sink limitations in species with different phenological types. To answer these questions, it is important to have reliable estimates of NSC age and transit time distributions.

Representing carbon allocation in compartmental systems is fundamental to make estimates of NSC age and transit time distributions (Ceballos-Núñez *et al.*, 2018; Metzler *et al.*, 2018; Metzler & Sierra, 2018). By compartmentalizing two whole-tree carbon allocation models proposed by Klein & Hoch (2015) and Ogle & Pacala (2009), and estimating the age and transit time distributions based on the mathematical framework developed by Metzler & Sierra (2018) and Metzler *et al.* (2018), we address here three main questions: **i)** How different are the predictions of NSC dynamics between tree tissues and trees of species representing different functional types? **ii)** What is the predicted age structure of the NSC reserves available to sustain tree metabolism under carbon limitation and for how long can these reserves last? And **iii)** what are the main carbon fluxes that have a larger influence on the NSC mean age and mean transit time? We expect these compartmental models, which consider organ specific and compound specific carbon pools, to allow us to estimate differences in the NSC age distributions of trees with different life strategies, and to associate them with different storage traits. We also expect that by estimating the changes of the NSC transit time during a severe carbon limitation condition, we can describe the age structure of the carbon available for sustaining the tree’s metabolism and growth, and to estimate how long can it take for the trees to exhaust their reserves depending on their NSC consumption level.

# Materials and Methods

## Models description

We used compartmental linear models of carbon allocation in individual trees for estimating NSC age and transit time distributions (Figs. 1 and 2). Compartmental models describe the exchange of mass between compartments following mass conservation principles (Jacquez & Simon, 1993; Metzler & Sierra, 2018). This means that: i) the mass of NSC leaving each compartment is a fraction of the mass of the NSC compartment, and ii) the mass entering the compartment is immediately mixed with the mass of the NSC compartment, making the mass of the compartment homogeneous at any time (Metzler & Sierra, 2018). The structures of the compartmental linear models follow those described in Klein & Hoch (2015) for *Pinus halepensis* Mill. and on Ogle & Pacala (2009) for *Acer rubrum* L. and *Pinus taeda* L. with small variations based on theoretical assumptions (Figs. 1 and 2). We estimated the model parameters (annual fraction of carbon transferred between pools) based on the carbon fluxes and pool stocks reported in the two studies for each species (Tables 2 and 1).

The model proposed by Klein & Hoch (2015) was parameterized using a carbon balance approach and exhaustive eco-physiological measurements during more than 13 years at Yatir forest, Israel. *P. halepensis* occurs in humid mediterranean regions, but Yatir forest is a semi-arid forest with only 285 mm of annual precipitation and an extended drought period of several months, so trees there are at the limit of the species’ growth requirements (Klein & Hoch, 2015). Model parameters were estimated for a typical mature, healthy tree where the amount of carbon fixed was assumed to be very close to the amount of carbon released, i.e., trees were close to steady state condition with respect to carbon (Klein & Hoch, 2015). Three organ specific carbon pools were defined as: stem, foliage and belowground; each with three compound specific carbon pools: starch (stored NSC), soluble sugars (active NSC) and structural carbohydrates (i.e., biomass) (Fig. 1). The starch and soluble sugars were assumed to be the stored (slow cycling pool) and active (fast cycling pool) NSC respectively, during model parameterization. All fluxes of carbon were reported in the original publication in grams of carbon per tree per day (gC d-1) and converted to grams of carbon per tree per year (gC yr-1). Then, the fluxes were transformed to the annual fraction of carbon that leaves each pool (yr-1) by dividing them by the carbon stock of the donor pool. These fractions were used as the parameters for the model (Fig. 1, Table 2).

Ogle and Pacala, (2009) proposed a mechanistic model named “Allometrically Constrained Growth and Carbon Allocation" (ACGCA). We used the ACGCA model to estimate the fluxes and pool sizes of the model in Figure 2 for a typical mature healthy tree of each species (*A. rubrum* and *P. taeda*) at steady state (Table 1). The parameters for steady state were obtained after running the ACGCA model for 700 time steps, to the point where pool sizes and fluxes did not change with time. ACGCA estimates the pool stocks in grams of glucose per tree (gGluc) and the fluxes in grams of glucose per tree per year (gGluc yr-1). Here, we converted these parameter values to grams of carbon (gC) and grams of carbon per year (gC yr-1) respectively, based on the molar masses of carbon and glucose (12 and 180.15 g mol-1, respectively). Then, the model parameters were also calculated by dividing the flux value by the size of the compartment from which C was removed, obtaining annual fraction of carbon leaving each pool.

The ACGCA model was designed to estimate growth and reproduce a range of physiological states defined by tree’s allometries and labile carbon (NSC) status (Ogle & Pacala, 2009). The model we used for our estimations and simulations follows a linear compartmental interpretation of the ACGCA model, based on a carbon balance approach. This model is structurally similar to the one used for *P. halepensis*: It considers organ specific carbon pools as foliage, branches and coarse roots, stem, and fine roots; and compound specific carbon pools as transient NSC, active NSC, stored NSC, and structural carbohydrates per tree organ (Fig. 2). Nevertheless, the chemical nature of the carbon in these pools is restricted to glucose; no differentiation between starch and sugar is made.

These models are described with a system of ordinary differential equations expressed in the general linear non-autonomous form presented in Ceballos-Núñez *et al.*,(2018) (equation 1):

(1)

where is the vector of rates of change of carbon with respect to time in each compartment; is a square matrix where is the number of compartments in the model, the diagonal elements of the matrix are the fraction of carbon leaving each pool and the off-diagonal entries represent the fraction of carbon transferred among compartments; is the vector of mass of carbon in each compartment; is the vector of partitioning of the photosynthetic input ; and is a vector of initial values of the carbon compartments.

## Estimation of NSC ages and transit times of mature healthy trees (close to steady state)

We estimated the age and transit time distributions for the models described above at steady state, which we interpret here as the condition of mature healthy trees, whose carbon uptake is nearly balanced by respiration and litter fall. These distributions were calculated as the sum of exponential distributions using the formulas developed by (Metzler & Sierra, 2018). The age density distribution of the carbon that is in the system is given by the probability of finding carbon particles of a certain age () and it follows the equation

(2)

where is the vector of release rates from the system, is the matrix exponential evaluated at age , and interpreted as the probability matrix of transfers among compartments, is the distribution of carbon among the different pools, and is the steady-state content of the system (equation 1). We use here the symbol to represent the vector norm, which is the sum of the absolute values of all entries of the vector.

The mean age is given by the expected value ()

(3)

Transit time can be considered as forward transit time (FFT) or backward transit time (BTT) (Metzler *et al.*, 2018). The FFT is the time a particle would take to travel the system after its arrival at a given time. The BTT is the age that a particle has when it leaves the system. Therefore, the BTT density distribution () describes the probability that a carbon particle has a certain age when it leaves the system at time . As the aims of this paper concern the age of the carbon when it leaves the system as respired CO2, we will deal here with the BTT only expressed as:

(4)

The mean backward transit time is defined as ():

(5)

Note that the definitions presented here can only be applied to autonomous systems at steady state (Metzler & Sierra, 2018). Therefore, these formulas were used to characterize the NSC dynamics of mature healthy trees where the carbon inflow and the coefficients in (the fraction of carbon transferred between pools) do not change over time. To characterize NSC dynamics, the age and transit time distributions were calculated only for the NSC pools of the described models in Fig. 1 and Fig. 2.

## Estimation of NSC ages and transit times of trees under carbon source limitation (out of steady state)

We estimated time-dependent NSC age and transit time distributions for every year after the assimilation input was set to zero, but keeping the transfer carbon coefficients (matrix ) constant. We used zero assimilation to have a clear view of how trees use their NSC when they depend exclusively on stored NSC. This approach allowed us to evaluate how limitations in carbon assimilation would impact the age and transit time distributions of carbon in mature healthy trees. The changes in these quantities reflect how old the remaining NSC reserves are, and how old is the carbon used for respiration is at each time step.

In our simulations, we maintained the assimilation flux constant at the levels reported for healthy trees in steady state (Table 2) for the first 10 years (), and then set it to zero in any subsequent time . Until , the NSC age and transit time distributions and did not change. These distributions constitute the initial (steady state) conditions for the system prior to the disturbance. The mathematical framework for estimating the age and transit time densities when the elements of the system (equation 1) depend on time, and are out of steady state, was developed by Metzler *et al.,* (2018). We therefore estimated the NSC age and transit time densities for the subsequent times using the formulas described in Metzler *et al.* (2018). We used the python packages “bgc-md” and “CompartmentalSystems”, which implement the formulas required for these computations.

## Sensitivity and uncertainty of the NSC mean age and mean transit time to variations in sink strength

To understand the sensitivity of the NSC mean age and mean transit time to changes in the sink carbon fluxes, we evaluated the change in NSC mean age and mean transit time to a given numerical alteration of the fraction of carbon leaving each pool (coefficients of matrix in equation 1). This analysis allowed us to identify the pool-specific fluxes that have a larger influence on the overall NSC age and transit time in mature trees. For that, we used the method “Elementary Effects” (Morris, 1991; Campolongo *et al.*, 2007). This method analyzes the change in model output if exactly one parameter is changed by a random fraction between L levels (150) of its feasible range. It then changes each parameter once and repeats this process throughout p+1 simulations that are called a “trajectory” in the parameter space (Cuntz *et al.*, 2015). The parameter space was estimated based on the parameter variability provided by Klein & Hoch (2015) and Ogle & Pacala (2009). Then, we ran 100 trajectories in this parameter space. We estimated a bigger parameter space than the one reported for the species to capture a more general trend out of the limits of each species. Then, the Elementary Effect of each parameter in each trajectory is calculated as a differential quotient

(6)

where is as a fraction of the range. The mean and the variance of the absolute values of the from the 100 trajectories were used as a measure of sensitivity (Cuntz *et al.*, 2015). The Elementary Effects simulations and calculations were done using the R packages “sensitivity V1.15.2“ (Pujol *et al.*, 2017) and ”SoilR" (Sierra *et al.*, 2014).

To evaluate how the uncertainty in the models’ parameters affects the mean age and the mean transit time of the species evaluated, a Monte Carlo Simulation (MCS) analysis was performed. This method involves repeated model realizations of a random selection of parameter values within the assumed parameter space (Parkinson & Young, 1998). We used only the most influential parameters in the models output to propagate the uncertainty. The variability associated with each parameter has been derived from Klein & Hoch (2015) for *P. halepensis* and Ogle & Pacala (2009) for *A. rubrum* and *P. taeda*. We assumed that these parameters come from independent Gaussian distributions. This assumption of independence is potentially limiting given that the MCS analysis would yield different results if there were covariance between the parameters. However, the degree of association between parameters is unknown to us, but if better information on their correlation would be available, this uncertainty could be re-estimated.

# Results

## NSC ages and transit times of mature healthy trees (trees close to steady state)

Different NSC age distributions were evidenced between tree species (Fig. 3). The mean NSC transit time -the age of the carbon being used in metabolism and growth- for *P. halepensis* was very low (0.49 ± 0.08 years). Likewise, the overall mean NSC age (the age of the carbon remaining in the tree) was also very low (0.98 ± 0.38 years), In contrast, the temperate species *A. rubrum* and *P. taeda* had slower predicted carbon cycling with mean ages of 9.45 ± 3.7 and 4.4 ± 0.72 years and transit times of 2.95 ± 0.31 and 2.4 ± 0.09 years, respectively. The difference between mean age and mean transit time was considerably bigger for *A. rubrum* (6.5 years) than for *P. taeda* (2 years), which indicates that the former stores the carbon longer.

The predicted NSC age and transit time distributions among trees’ organ- and compound-specific compartments showed contrasting behaviors. NSC age distributions for all the NSC pools in *P. halepensis* were slightly similar across tissues (Fig. 3, Table 3). For this species, the NSC stored in stem and roots had the oldest mean ages, around 1.55 ± 0.58 years old. In contrast, there was a clear distinction in the predicted mean ages of active and stored NSC pools for the temperate species *A. rubrum* and *P. taeda* (Table 3). The NSC stored in the stem had a mean age of 21.3 ± 5.38 years in *A. rubrum,* but only 14.2 ± 1.63 years in *P. taeda*. On the contrary, the mean ages of NSC stored in the foliage and fine roots (FSNSC and RSNSC pools) were lower in *A. rubrum* (3.5 ± 0.20 and 2.5 ± 0.20 years respectively) than in *P. taeda* (5.2 ± 0.06 and 4.19 ± 0.06 years, respectively, Table 3). Overall, the age of the NSC in each tree organ is given by the combination of the NSC ages of the compound specific compartments -active, stored and transient NSC pools- in each respective organ. Mean age estimates of the NSC in leaves and fine roots are less than two years (Table 4). In the stem, mean ages of NSC were 0.73 ± 0.58, 9.97 ± 5.38 and 4.58 ± 1.63 years for *P. halepensis, A. rubrum and P. taeda* respectively (Table4).

NSC age and transit time distributions characterized in detail the age composition of the NSC that remains in and leaves the tree (Figs. 3 and 5). The mixture of NSC ages for mature healthy trees followed a phase type distribution (Fig. 3), which is a mixture of exponential distributions (Metzler & Sierra, 2018). The shape of the distributions depended on the speed at which the carbon was cycled within the tree. For *P. halepensis*, 95% of all NSC in the entire tree was younger than 3.3 years. For *A. rubrum*, 95% of the NSC was less than 42 years old, and NSC respired or allocated to growth did not exceed 2.9 years. In *P. taeda*, 95% of all NSC was less than 20 years old, but the 95% of NSC that leaves the system was younger than 2.4 years old. The trees’ NSC pools had different NSC age and transit time compositions (Fig. 3), which characterize the different dynamics of each NSC compartment in the trees’ carbon balance.

## NSC ages and transit times of trees under carbon source limitation (out of steady state)

When simulating source limitation by setting carbon assimilation to zero for the trees characterized in Fig. 3, our model predicted changes in the shape of the NSC age and transit time distributions over time due to NSC storage mobilization (Fig. 4 and Fig. 5). The simulated starvation progressively reduced the NSC masses from storage compartments (Fig. 4). The carbon mass that is drawn from the storage was proportionally younger during the initial phase of the simulations in comparison to the more advanced phases of the simulations (Fig. 5). Therefore the proportion of young carbon decreased rapidly over time, flattening the entire NSC age distribution of the trees (Fig. 4). Consequently, both the mean age and mean transit time of the NSC increased. The mean transit time increased first in an exponential way and then increased linearly (Fig. 6). The exponential phase explains the progressive and fast depletion of the reserves as the proportion of young carbon decreased faster than the proportion of old carbon. Then, when the age distribution of the remaining NSC becomes increasingly uniform, the linear phase describes the aging of the carbon.

The increase in mean transit time over time indicates that trees used increasingly older reserves for respiration as the storage pool was exhausted. For trees that can store carbon for a longer time, such as *A. rubrum* and *P. taeda*, the stop in the assimilation rate resulted in an increase in the mean transit time of several years, due principally to the availability of several decades old NSC in the stem and coarse roots (Fig. 3). For these species, the mean transit time increased from 2.9 years old in healthy conditions to 21 years old for *A. rubrum*, and from 2.4 to 13 years old for *P. taeda*, when trees already consumed around 80% of their reserves. If we consider consumption levels between 50 to 60% of the NSC the mean transit time raised to 10.3 ±4 years old for *A. rubrum* and to 5 ± 1.5 years old for *P. taeda* (Fig. 6). It took around 5 years for them to consume 80% of their reserves and 3 ± 1 years to consume 50% (Fig. 6). In contrast, for *P. halepensis* trees growing in Yatir forest, the transit time increased from 0.48 to 4 years old at the end of the exponential trend (Fig. 6) in just 2 years.

## Sensitivity and uncertainty of mean ages and mean transit times to variations in sink strength

The predicted mean age and the mean transit time of NSC were similar in terms of their sensitivity to changes in the tree carbon cycling rates for all tree species. The mean age was mainly sensitive to changes in the consumption of NSC from stored carbon in the stem, branches and coarse roots (Cs) and the loss of NSC in the transition from sapwood to heartwood (LSs) (Fig. 7). The mean transit time was principally sensitive to the allocation of NSC to storage in the roots (Sr and Sbr) and to root growth (Gr). In addition, both quantities were sensitive to changes to the allocation to root active NSC (Stor and BRl) and to root respiration (Rr) to a lesser degree (Fig. 7). The impact of changes in these cycling rates on the mean age and mean transit time is complex and non-linear in some cases (Fig. 8). But in general, the higher the consumption from the NSC stem pools the younger is the NSC in the tree; and the higher the storage in the NSC in the roots the older the NSC in the tree.

The uncertainty in the mean ages and in the mean transit time associated with the uncertainty in the most influential cycling rates, described above, was smaller than the mean differences between species. In general, *A. rubrum* had higher uncertainties than *P. taeda* and *P. halepensis* (Fig. S1). Some very exceptional high mean ages of the NSC are expected in very rare combinations of parameter values at the very limit of their distributions (Fig. S1).

# Discussion

The whole-tree compartmental models for carbon allocation tested here allowed us to estimate: i) differences in the NSC age and transit time distributions that reflected carbon storage dynamics of different tree species; ii) the change in the age of the NSC used under limited assimilation; and iii) the main NSC cycling rates that influenced the NSC mean age and mean transit time in mature trees.

The predicted NSC age and transit time distributions showed differences between tree species, depending on their functional type: deciduous (*A. rubrum*) or evergreen (*P. taeda*); and their growth environment: highly limited (mediterranean *P. halepensis*) and mesic growth conditions (temperate species) (Fig. 3). These differences reflected the timescale (for how long) and the location where trees accumulate their reserves. For instance, *A. rubrum* had the higher mean age and a higher quantity of old carbon stored, evidenced in the longer tail of the NSC age distribution in comparison to *P. taeda* and *P. halepensis* (Fig. 3). This age distribution of the NSC within each pool quantifies the abundance of carbon in each age class per NSC pool, and characterizes the role of each NSC pool in carbon cycling and storage of mature trees. For the temperate species, NSC was stored longer in the stem and coarse roots (SSNSC) where the mixture of NSC ages was more abundant in old carbon (Fig. 3). On the contrary , *P. halepensis* did not show differentiation between slow (stored NSC) and fast cycling (active NSC) pools (Fig. 3) suggesting no capacity for long-term storage of NSC. However, it may also be possible that long-term storage pools where neglected by the assumptions made in this model.. These results are consistent with the difficulties of separating and measuring NSC pools, and highlight the utility of estimating NSC ages based on compartmental systems to identify and understand the carbon dynamics associated to these elusive carbon pools. Our results predict different carbon storage traits between tree species that range from slow carbon cycling trees that accumulate larger proportions of long term reserves (e.g., *A. rubrum*) and fast carbon cycling trees with low accumulation of long term reserves (e.g., *P. halepensis*).

NSC transit time distributions reflect the age composition of NSC reserves being used by trees in metabolism and growth. Our estimates showed that healthy trees used mainly young carbon (Fig. 5). The allocation of mainly young carbon to respiration and growth in mature healthy trees has been already documented (Carbone *et al.*, 2013; Muhr *et al.*, 2018). This behavior has been commonly explained by the “last in, first out” hypothesis for using the NSC where the most recently fixed carbon entering the systems is the one that is used at first (Dietze *et al.*, 2014; Hartmann & Trumbore, 2016). In our models, this idea is partly represented by the differentiation between fast and slow NSC cycling pools in each tissue. This differentiation in organ NSC pools and compound NSC pools (fast and slow cycling pools) represents the spatial heterogeneity of the NSC ages within the tree. Partly in disagreement with the ‘last in, first out’ principle, previous studies have also shown that some old NSC is mixed in the metabolized CO2 in healthy trees with non-limiting assimilate supply, due to the continuous exchange of carbon between the active NSC and the stored NSC pools (Richardson *et al.*, 2012; Carbone *et al.*, 2013; Muhr *et al.*, 2013). This is in agreement with our results where the NSC transit time distributions (Fig. 5) showed that the carbon being used in metabolism and growth is a mixture of carbon of different ages. The transit time distribution is mainly determined by the age structure of the largest carbon source and the balance between carbon sources and sinks in the tree. In this sense, in healthy-mature trees the inflow of new carbon greatly exceeds the retrieval of old stored carbon for sustaining metabolism and growth, which leads to the high abundance of young NSC in the trees and skewness of the distribution towards low values, with corresponding low values of mean transit time (Fig. 3, Fig. 5). Therefore, within our framework, healthy trees may use mainly young carbon due to its high abundance in the NSC pools, and its constant replenishment due to rapid assimilation of atmospheric carbon, and not because the younger carbon is more available due to its position in the tree. This concept is supported by the simulation results in Fig. 4 where the young carbon is depleted faster than the old carbon -due to its relative high abundance- until eventually flattening the age distribution of the NSC in each pool.

In other words, our results provide a probabilistic interpretation for the use of young carbon for metabolism and growth. Since young NSC is more abundant in storage pools, it has a larger probability of being used for plant function. These results provide a new perspective on the understanding of the NSC allocation to metabolism and growth and also highlight the utility of obtaining the NSC transit time distribution in mature trees for understanding carbon source/sink imbalances.

Under severe carbon limitation, the trees used their NSC reserves and consequently the NSC mean transit time increased rapidly (Fig. 6). Previous experiments that interrupted carbon assimilation either by girdling, harvesting of the main trunk, or hurricane damage, also reported a rapid increase in the NSC mean transit time from very young to several years old carbon. For instance, 14CO2 respired from *Scleronema micranthum*, a measure of transit time, increased from 1 to 15 years old after girdling (Muhr *et al.*, 2018); stump resprouts in *A. rubrum* growing after trunk harvesting were found to be made of carbon up to 17 years old (Carbone *et al.*, 2013); and up to 10 years old carbon was used to grow new roots for tropical trees after a hurricane damage (Vargas *et al.*, 2009).

We were able to describe how this old carbon was used and for how long it could last by observing how the NSC mean transit time increased over time during our simulations. The NSC mean transit time increased in an exponential way that depended on the amount and the cycling speed of the reserves, followed by a linear phase that occurred when the NSC age distribution got flat and only described the aging of the remaining NSC (Fig. 6). The exponential increase in the NSC mean transit time described how the trees consume between 80 and 90% of the available carbon, depending on their storage strategy. The NSC mean transit times towards the end of this period of exponential increase was higher (14-21 years) than the reported (12-17 years) age of the respired CO2 of trees subjected to starvation (Carbone *et al.*, 2013; Muhr *et al.*, 2018). This difference can be explained by the fact that we did not represent mortality explicitly; therefore, the trees continued using reserves for a longer time than in experiments where the trees die before exhausting 80-90% of their reserves. Considering a consumption threshold between 50 to 60% (Mei *et al.*, 2015; Wiley *et al.*, 2019), the mean transit time falls to 5 and 10 years for *P. taeda* and *A. rubrum,* respectively. Our predictions also report a very slow consumption of the reserves when trees are under carbon starvation, taking between 2 to 5 years to exhaust 80% of their reserves, and between 1 to 3 years to reach the 50-60% of NSC consumption. Measurements in mature trees documented an up to three times faster increase in the NSC mean transit time than in our model (Carbone *et al.*, 2013; Muhr *et al.*, 2018). These discrepancies could be due to several reasons: i) The parameters provided for our models may not fully represent the trees evaluated in the studies, more precise and exhaustive parameter estimation may be needed; ii) the measurements may have been taken for trees that have not reached yet their steady state and therefore have higher transfer coefficients of carbon between pools; iii) additional fluxes and carbon compartments not considered in the model, plus other mechanisms not considered such as trees’ ability to control growth and respiration under stress, active NSC allocation to storage, or other non-linearities in the model; iv) our source limitation simulations were restricted only to a complete cease of carbon assimilation. Limiting conditions such as drought or severe physical damage, also may imply a limitation in the mobilization of the stored NSC or truncation of the NSC mass, which would reduce the quantity of stored NSC available and cause a quicker depletion of the NCS in the trees; and/or v) measurements of respired 14CO2 in previous studies is restricted to the stem-wood and thus do not reflect the time that the increase in the mean NSC transit time would take for the whole tree. Overall, this analysis allowed us to estimate the age composition of the NSC reserves being used at any point of the source limitation event and the time that each tree would take to exhaust those reserves.

Along with source variability, sink strength also plays a fundamental role in NSC dynamics of mature trees. It is reflected in the NSC mean age and mean transit time if the assimilation of carbon is kept constant and numerical changes are induced in the cycling rates between carbon pools. The sensitivity analysis estimated that the efflux rate of carbon from the storage in the stem and the cycling rates of roots have a large influence on the NSC mean age and mean transit time, playing an important role in NSC dynamics (Fig. 7). Previous studies have shown the important contribution of the stored NSC in the stem and roots to the respired CO2 of trees under stress (Carbone *et al.*, 2006; Richardson *et al.*, 2012; Muhr *et al.*, 2013, 2018; Hartmann *et al.*, 2018), and the important contribution of belowground storage to tree recovery after a disturbance (Schutz *et al.*, 2009; Hagedorn *et al.*, 2016; McDowell *et al.*, 2018). These allocation rates usually change when trees experience outstanding limiting conditions (Nogués *et al.*, 2006; Wiley *et al.*, 2013, 2019; Hagedorn *et al.*, 2016), but the mechanism behind these changes remains uncertain (Chesney & Vasquez, 2007; Gaudinski *et al.*, 2009; Hartmann *et al.*, 2013; Mei *et al.*, 2015). When modeling carbon allocation as compartmental systems, we should be aware that changes in the fluxes between compartments can be due to changes in the compartment mass only (mass conservation principle) or changes in the cycling rates (transfer coefficients of the matrix B) of the trees. In our simulations, as far as the transfer coefficients remained constant, changes in the fluxes after the disturbance were due to changes in the mass of the compartments. However, a change in NSC dynamics happens when the cycling rates change independently of the system carbon mass, which would change the carbon transfer coefficients between pools. For instance, increasing the allocation rates from the storage in the wood to growth or respiration (Cs) would make the trees to cycle carbon faster, build younger reserves during their productive and healthy conditions, and increase the tree’s vulnerability to starvation; while increasing the allocation of carbon to storage in the roots (Sr) would make them slower cyclers, build older reserves and be more resilient to low productivity periods (Fig. 8). Based on our models, we have estimated how cycling rates drive the NSC age and transit time distributions of mature trees, but it is still unclear what physiological and environmental factors alter this carbon allocation parameters and what those changes imply for the use of carbon reserves by trees under limiting conditions.

# Limitations and conclusions

Comparisons between the estimated NSC mean age and mean transit time with empirical measurements can serve as important diagnostics for model evaluation (Ceballos-Núñez *et al.*, 2018). However, this type of models may not be easy to parameterize and may require a large number of observations. Our model parameters are rough estimates of the fluxes for an average healthy mature tree of each species (ACGCA model) or population of trees (*P. halepensis* case). They are constrained by the assumptions made when the parameters were estimated, e.g., the NSC allocation to storage happens passively when carbon supply exceeds demand. These parameter estimates can be improved with empirical research, theoretical studies, and statistical approaches that consider variability within and among trees as well as alternative assumptions regarding NSC allocation. Furthermore, our representations are very simple and do not consider nonlinear interactions and other important fluxes, such as the exchange of carbon with the rhizosphere (Epron *et al.*, 2011), allocation of carbon to reproduction (Hacket-Pain *et al.*, 2018), emissions of biogenic volatile organic compounds (BVOC) (Epron *et al.*, 2012), and allocation to defense compounds (Huang *et al.*, 2019a), which also play an important role for determining NSC dynamics. However, information about these fluxes is still scarce and uncertain. Nevertheless, our results open the possibility to better understand NSC dynamics in mature trees based on estimated NSC ages and transit times in different tree organs of species with contrasting life strategies and growth environments. Our estimates are relevant in: characterizing general differences in the NSC dynamics in contrasting tree species, identifying different storage traits based on plant type and growth environment; predicting the way how trees use their reserves, 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 disturbance; and identifying the determinant sink fluxes in NSC dynamics for mature trees.

# Acknowledgements

We want to thank Markus Müller for important support given in writing the code for running the models and simulations. This work was supported by the GIF (German Israeli Fund) funding Grant number I-1334-307.8, the German Research Foundation through its Emmy Noether Program (SI 1953/2–1), and the German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, D- 04103 Leipzig.

# Author Contribution

CS and DH conceived the idea. All authors contributed with the design of the work. DH performed the computations and wrote the manuscript. All authors revised the manuscript and gave important and critical input.

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# Figures and tables

**Figure 1:** Compartmental representation for the carbon allocation model proposed for the evergreen mediterranean *Pinus halepensis* by Klein and Hoch (2015). The squared compartments define the state variables, and the arrows define the fraction of carbon that is transferred between pools. The name of the fluxes and state variables are defined in the Tables 1 and 2.

**Figure 2:** Compartmental representation for carbon allocation proposed for the temperate deciduous *Acer rubrum* and evergreen *Pinus taeda* species based on a theoretical interpretation of the ”ACGCA” developed by Ogle and Pacala (2009). The squared compartments define the state variables, and the arrows define the fraction of carbon that is transferred between pools. The name of the fluxes and state variables are defined in the Tables 1 and 2.

**Figure 3:** Age distribution of the non-structural carbon in the trees and in 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.

**Figure 4:** Age distribution of the non-structural carbon in the whole tree for some subsequent years of the disturbance simulation for each of the species *Pinus halepensis*, *Acer rubrum* and *Pinus taeda*.

**Figure 5:** Backward transit time distribution of the non-structural carbon in the whole tree for some subsequent years of the simulated disturbance for each of the species *Pinus halepensis*, *Acer rubrum* and *Pinus taeda*. Year 0 represents the backward transit time of the healthy mature trees that have not experienced any disturbance.

**Figure 6:** Non-structural carbon mean backward transit time and NSC consumption during 50 years of the disturbance simulation for each species *Pinus halepensis*, *Acer rubrum* and *Pinus taeda*. After leaving the trees the first 10 years growing under healthy conditions, the productivity was set to zero for the subsequent 40 years.

**Figure 7:** 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 bigger the mean sensitivity value the more sensible is the mean age or the mean transit time to changes in that flux. The fluxes are labeled as they are defined in Table 2.

**Figure 8:** Association between the most sensitive NSC fluxes (Tab 2) and the mean age and mean transit time for each species: *Pinus halepensis*, *Acer rubrum* and *Pinus taeda*.

**Table 1:** Compartments description for the models used, with structure as depicted in Figs 1 and 2.

|  |  |
| --- | --- |
| Abbreviation | Name |
| E | Transient Carbon Pool |
| FANSC | Foliage Active Non Structural Carbon |
| FSNSC | Foliage Stored Non Structural Carbon |
| FB | Foliage Biomass |
| BRANSC | Branches and Coarse Roots Active Non Structural Carbon |
| BRB | Branches and Coarse Roots Biomass |
| SANSC | Stem Active Non Structural Carbon |
| SB | Stem Biomass |
| SSNSC | Stem stored Non Structural carbon |
| RANSC | Fine Roots Active Non Structural Carbon |
| RSNSC | Fine Roots Stored Non Structural Carbon |
| RB | Fine Root Biomass |

**Table 2:** Annual rates of carbon cycling (year−1) and other parameters for each species from the models in Figs. 1 and 2 for the species under investigation *Pinus halepensis* (model from Klein and Hoch 2015)*, Acer rubrum* and *Pinus taeda* (ACGCA model from Ogle and Pacala 2009). Pool name abbreviations are defined in the Table 1

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Abbreviation | Parameter Name | *P. halepensis* | *A. rubrum* | *P. taeda* |
| A | Assimilation at steady state | 23520 | 211770 | 200090 |
| Rm | Maintenance respiration |  | 0.250 | 0.167 |
| Fl | Allocation to FANSC |  | 0.050 | 0.042 |
| BRl | Allocation to BRANSC |  | 0.669 | 0.757 |
| Sl | Allocation to SANSC |  | 1.00E-04 | 6.24E-06 |
| Rl | Allocation to RANSC |  | 0.031 | 0.035 |
| Rf | Respiration foliage | 9.560 |  |  |
| Rbr | Respiration branches and roots |  |  |  |
| Rs | Respiration stem | 0.590 |  |  |
| Rr | Respiration stem | 16.840 |  |  |
| Gf | Growth foliage | 2.940 | 0.939 | 0.932 |
| Gbr | Growth branches and coarse roots |  | 0.912 | 0.943 |
| Gs | Growth stem | 0.300 | 0.912 | 0.943 |
| Gr | Growth roots | 1.280 | 0.893 | 0.942 |
| Lf | Litterfall foliage | 0.340 | 1.000 | 0.333 |
| Lbr | Litterfall branches and roots |  | 0.047 | 0.047 |
| Lr | Literfall fine roots | 0.070 | 1.000 | 0.500 |
| LSs | Stored NSC lost in wood conversion to heartwood and litter fall | 0.003 | 0.031 | 0.060 |
| Sf | Allocation to storage in foliage (FSNSC) | 0.440 | 0.061 | 0.068 |
| Sbr | Allocation to storage in stem from branches and coarse roots (SSNSC) |  | 0.088 | 0.057 |
| Ss | Allocation to storage in stem (SSNSC) | 0.800 | 0.088 | 0.057 |
| Sr | Allocation to storage in roots (RSNSC) | 4.980 | 0.107 | 0.058 |
| Cf | Allocation from storage in foliage (FSNSC) to E | 2.020 | 1.000 | 0.333 |
| Cs | Allocation from storage in stem (SSNSC) to E | 1.090 | 0.023 | 0.023 |
| Cr | Allocation from storage in roots (RSNSC) to E | 1.220 | 1.000 | 0.500 |
| FtoS | Allocation from foliage to stem | 33.700 |  |  |
| StoF | Allocation from stem to foliage | 0.040 |  |  |
| Stor | Allocation from stem to roots | 3.150 |  |  |
| rtoS | Allocation from roots to stem | 0.110 |  |  |

**Table 3:** Mean ages for the different pools and species (*Pinus halepensis, Acer rubrum* and *Pinus taeda)* in units of years.

|  |  |  |  |
| --- | --- | --- | --- |
| Pool name | *P. halepensis* | *A. Rubrum* | *P. taeda* |
| E |  | 1.55 ± 0.20 | 1.19 ± 0.06 |
| FLNSC | 0.03 ± 0.001 | 2.55 ± 0.20 | 2.19 ± 0.06 |
| FSNSC | 0.52 ± 0.001 | 3.56 ± 0.20 | 5.22 ± 0.06 |
| SLNSC | 0.045 ± 0.10 | 2.55 ± 0.20 | 2.19 ± 0.06 |
| SSNSC | 1.370 ± 0.58 | 21.3 ± 5.38 | 14.22 ± 1.63 |
| RLNSC | 0.730 ± 0.76 | 2.55 ± 0.20 | 2.19 ± 0.06 |
| RSNSC | 1.550 ± 0.12 | 3.55 ± 0.20 | 4.19 ± 0.06 |

**Table 4:** Mean ages for the different organ specific pools (*Pinus halepensis, Acer rubrum* and *Pinus taeda)* in units of years.

|  |  |  |  |
| --- | --- | --- | --- |
| Pool name | *P. halepensis* | *A. Rubrum* | *P. taeda* |
| Leaves | 0.07 | 1.98 | 1.91 |
| Stem | 0.73 | 9.97 | 4.58 |
| Roots | 1.33 | 2.01 | 2.36 |