Ideas and perspectives: Allocation of carbon from Net Primary Production in models is inconsistent with observations of the age of respired carbon

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Abstract. Carbon allocation in vegetation is an important process in the terrestrial carbon cycle; it determines the fate of photo-assimilates and it has an impact on the time carbon spends in the terrestrial biosphere. Although previous studies have highlighted important conceptual issues in the definition and metrics used to assess carbon allocation, very little emphasis has been placed on the distinction between allocation of carbon from gross primary production (GPP) versus allocation from net primary production (NPP). An important number of simulation models and conceptual frameworks are based on the concept that C is allocated from NPP, which implies that C is respired immediately after photosynthetic assimilation. However, empirical work that estimates the age of respired CO_2 from vegetation tissue (foliage, stems, roots) shows that it may take from years to decades to respire previously produced photosynthates. The transit time distribution of carbon in vegetation and ecosystems, a metric that provides an estimate of the age of respired carbon, indicates that vegetation pools respire carbon of a wide range of ages, on timescales that are in conflict with the assumption that autotrophic respiration only consumes recently fixed carbon. In this contribution, we attempt to provide compelling evidence based on recent research on the age of respired carbon and the theory of timescales of carbon in ecosystems, with the aim to promote a change in the predominant paradigm implemented in ecosystem models where carbon allocation is based on NPP. In addition, we highlight some implications for understanding and modeling carbon dynamics in terrestrial ecosystems.

1 Introduction

Carbon that enters the terrestrial biosphere through photosynthesis may have very different fates depending on where this carbon is allocated in plants (Trumbore, 2006). Most of the organic carbon in the biosphere returns to the atmosphere in the form of CO_2 via respiration from autotrophic and heterotrophic organisms. The time it takes for assimilated carbon to return to the atmosphere depends strongly on what plant part or chemical compound the carbon is allocated to (Rasmussen et al., 2016; Luo et al., 2017; Lu et al., 2018; Herrera-Ramírez et al., 2020). For example, simple sugars may be used quickly for catabolic activity and appear in the respiration flux only a few hours after their biosynthesis, or they may be used to build structural

compounds that can remain stored as biomass for years to decades (Hartmann and Trumbore, 2016). Some of the biomass can be transferred to the soil as litter or via root exudation where it can stay as soil organic matter for even longer periods of time. During the time carbon is stored in the terrestrial biosphere, it does not contribute to the atmospheric greenhouse effect

25 (Neubauer and Megonigal, 2015; Sierra et al., 2021a); therefore, it is of fundamental importance to study carbon allocation and the time carbon stays in ecosystems to improve our understanding of interactions and feedbacks between the terrestrial biosphere and the climate system.

Despite recent advances in the understanding of physiological-level mechanisms of autotrophic respiration (Ra) and carbon allocation in plants (Hartmann and Trumbore, 2016), the representation of these processes in ecosystem and land-surface

30 models remains overly simplistic. These models are commonly used to predict interactions between the atmosphere and the terrestrial biosphere, but many of them represent autotrophic respiration as a constant proportion of gross primary production (GPP) (Figure 1). The remaining carbon (net primary production, NPP) is allocated to different plant parts according to specific partitioning coefficients (Franklin et al., 2012; Ceballos-Núñez et al., 2020). This approach appears pragmatic for modeling ecosystem-level carbon balances because it simplifies the representation of autotrophic respiration as a predetermined ratio of

35 GPP to carbon use efficiency (DeLucia et al., 2007). However, we argue here that for a more in depth understanding of the fate of photosynthates and the time carbon stays in ecosystems, Ra and carbon allocation functions need to be revisited in many models so to avoid predictions in conflict with empirical observations.

In individual plants, carbon allocation is a highly dynamic process that changes during plant ontogeny to allow them to respond to changes in the environment. The assumption that Ra is a fixed proportion of GPP does not allow accounting

40 for this dynamic (Collalti and Prentice, 2019). For example, when plants become carbon limited, as it may happen during environmental stress like drought, cold or defoliation, the proportional provision of carbon to Ra decreases, likely to free up resources to maintain allocation to defense (Huang et al., 2019a, b). Plant parts that are cut off from canopy photosynthate supply (and thus from GPP) via girdling respire carbon that is years to decades old (Muhr et al., 2013), where Ra is then fueled with carbohydrates that are stored in older tissues. During environmental stress, and during release of stress, belowground Ra

45 recovers faster than assimilation (Hagedorn et al., 2016), again highlighting a situation where Ra is decoupled from GPP.

A more mechanistic representation of Ra and carbon allocation in models would improve predictions of the dynamic response of terrestrial ecosystems to environmental changes. In particular, the source of the carbon (GPP or NPP) used for carbon allocation in models have consequences to predict the timescale of ecosystem responses as we will show here. Consequently, in this manuscript we: (1) review models and conceptual frameworks on the main approaches used to represent Ra

50 and carbon allocation at the ecosystem level; (2) show that models that allocate carbon from NPP and not from GPP predict a transit time equal to zero for the entire autotrophic respiration flux, or in other words, respired carbon from vegetation pools has an age (time since assimilation) equal to zero; (3) demonstrate that this prediction is inconsistent with measurements of the age of respired carbon obtained with radiocarbon measurements and does not capture the variability in the transit time of carbon within vegetation; (4) highlight that the choice of carbon allocation approach has consequences for predicting iso-

55 topic exchange fluxes with the atmosphere, to predict the transit time distribution of carbon in the terrestrial biosphere, and to incorporate radiocarbon measurements in model-data assimilation.
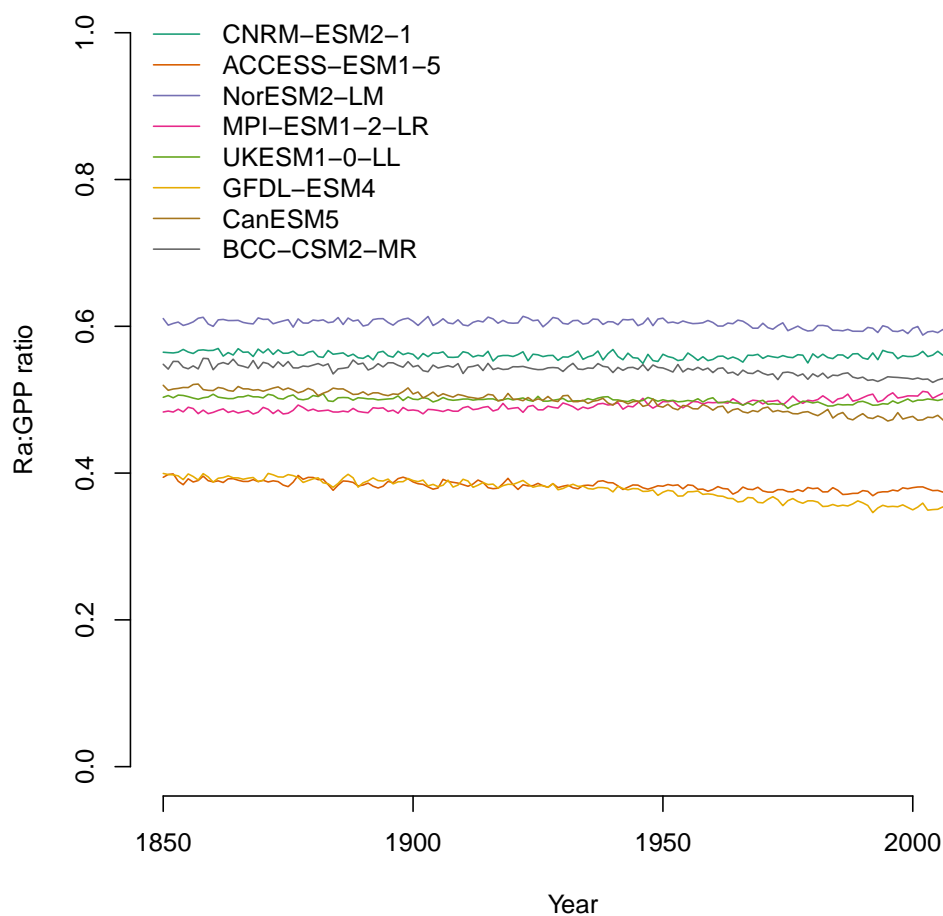
Figure 1. Ratio of autotrophic respiration Ra to gross primary production GPP at the global scale obtained from the historical simulations (*esm-hist*) of coupled carbon-climate models from the CMIP6 archive. Results from the majority of models suggest that Ra is represented as a constant proportion of GPP that does not change over time despite the increase in GPP predicted by all models.

2 Historical context, concepts, and models

2.1 Conceptual support for allocating carbon from NPP

A common assumption in ecosystem carbon models is that autotrophic respiration is a constant proportion of GPP. This assumption is based on the work of Waring et al. (1998), who found constant proportions between NPP and GPP in forest ecosystems, with a constant ratio NPP/GPP = 0.47, or Ra/GPP = 0.53. These constant ratios promoted a simplification in

the representation of production and growth in models, with NPP and autotrophic respiration often computed as a proportion (approximately 50%) of annual GPP. Synthesis studies have challenged the constancy of these ratios for different biomes, stand ages, climates, and soils (DeLucia et al., 2007; Collalti and Prentice, 2019). Despite criticisms, these simple ratios

65 continue being used as a practical approach to represent Ra in many ecosystem models, particularly if the research questions involved only concern net fluxes of carbon between ecosystems and the atmosphere, and not the processes involved in carbon assimilation, allocation to different tissues, and different forms of respiration.

Although a large proportion ($\sim 50\%$) of assimilated carbon may be respired on an annual basis from ecosystems as postulated by Waring et al. (1998), this carbon is not necessarily fixed from the current year or growing season. Instead, photo-assimilates

70 and structural tissues of different ages contribute to the total respiratory flux as we will see below.

Amthor (2000) identified three main paradigms generally used to conceptualize the process of autotrophic respiration: (1) the growth-and-maintenance-respiration paradigm (GMRP), (2) the growth-and-maintenance-and-wastage-respiration paradigm (GMWRP), (3) and the general paradigm (GP) that recognizes all possible processes that respiration might support.

These paradigms are very important to conceptualize the main processes of plant metabolism involved in respiration, but

75 they are not necessarily explicit about the source of carbon that would contribute to the respiration flux. For instance, one can implement a model that computes Ra following the GMWRP, but the actual carbon used for respiration can be subtracted directly from GPP following Waring et al.'s (1998) idea. Carbon would not enter any plant part, but still it would be respired following some physiological concepts.

Research on the matrix approach (Luo et al., 2017), which shows that one single equation generalizes the majority of existing

80 ecosystem and land-surface models, suggests that Ra is generally subtracted directly from GPP independently of the respiration paradigm implemented in the model. The matrix representation of Luo et al. (2017) can be written as

$$\frac{\mathrm{d}\boldsymbol{x}}{\mathrm{d}t} = U(t)\,\boldsymbol{b} - \xi(t)\mathbf{A}\,\mathbf{K}\,\boldsymbol{x}, \tag{1}$$

where $\boldsymbol{x}$ is a vector of ecosystem carbon pools, $U(t)$ is a function of carbon inputs to the ecosystem, generally obtained as $U(t) = \mathrm{GPP}(t) - \mathrm{Ra}(t) = \mathrm{NPP}(t)$. Then, NPP is allocated to ecosystem compartments such as foliage, wood, and be-

85 lowground biomass according to the vector of allocation coefficients $\boldsymbol{b}$. The product of the matrices $\xi(t)$, $\mathbf{A}$, and $\mathbf{K}$, is a compartmental matrix that has in its main diagonal the rates at which carbon is processed in each of the compartments, and in its off-diagonal the rates of carbon transfer among compartments. For vegetation compartments, 100% of all outputs (from mortality and litterfall) are transferred to litter and soil pools, because autotrophic respiration is already accounted for in the first term of equation (1). This modeling choice implies that the carbon used for autotrophic respiration never enters a particular

90 vegetation compartment and does not spend any time there (Figure 2).

In addition to modeling studies, the concept of quantifying carbon allocation after accounting for autotrophic respiration losses is also used in some empirical studies. For instance, the conceptual framework often used to analyze inventory data in tropical forests (e.g. Malhi et al., 2011, 2015) assumes that biomass growth results from the allocation of the products of NPP, after autotrophic respiration occurs. In this case however, carbon allocation is understood as *partitioning* of total NPP.

(a)

(b)
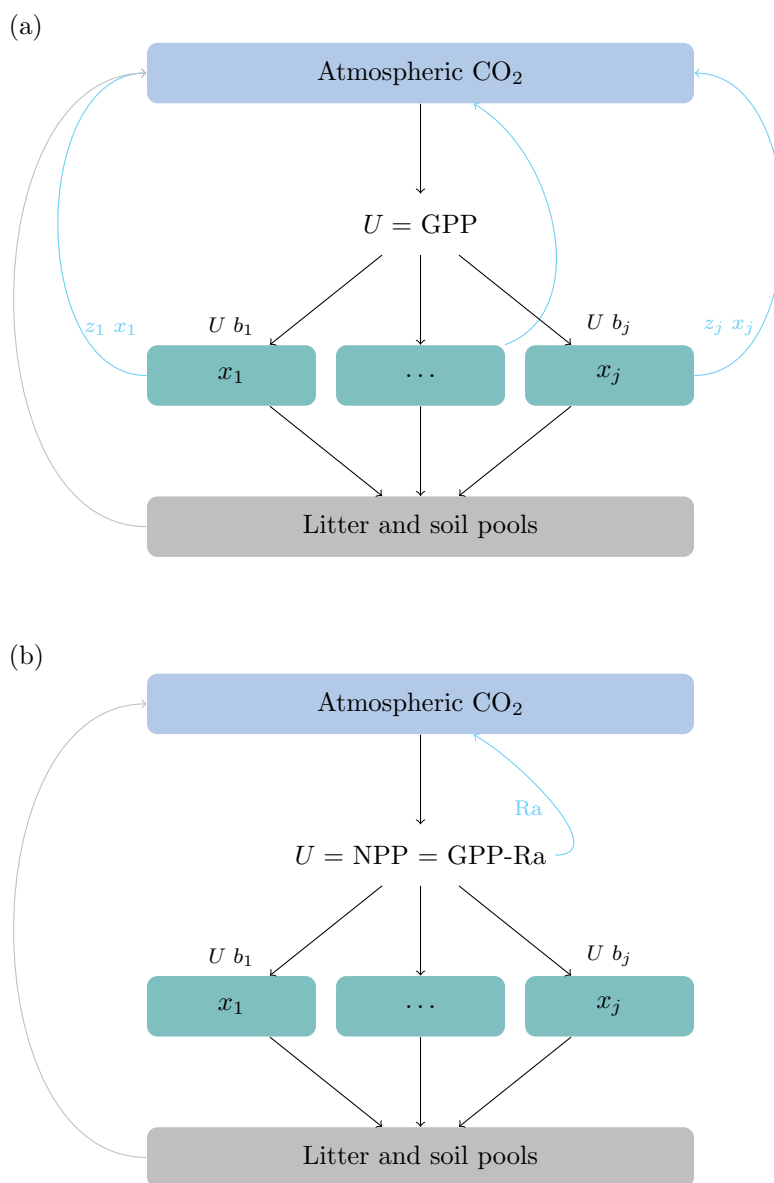
Figure 2. Conceptual diagram representing the difference between allocation schemes. (a) The source of carbon for allocation is GPP, split among the different vegetation pools $(x_1, \ldots, x_j)$ according to partitioning coefficients $(b_1, \ldots, b_j)$. The source of carbon for autotrophic respiration is the stock in the vegetation pools and it is computed according to the release coefficients $z_1, \ldots, z_j$ (see text for the definition of symbols). (b) The source of carbon allocation is NPP. In this case the functions used to obtain Ra may depend on the stock of carbon or nitrogen in vegetation pools, but Ra is subtracted from GPP before NPP is allocated. The carbon used for Ra never enters the vegetation pools and does not spend any time there.

95 Litton et al. (2007) showed that carbon allocation can be understood differently by different authors, as a flux, as biomass, or as partitioning of the total GPP flux. In the case of the tropical forest data, carbon allocation is understood as partitioning coefficients of the NPP flux and not partitioning of GPP as originally defined by Litton et al. (2007).

Together, these previous studies show that empirical work has promoted the implementation of Ra as a constant proportion of GPP, or based on some respiration paradigms, but subtracting Ra from GPP before carbon allocation occurs. Therefore
100 models compute first NPP and subsequently allocate the non-respired carbon to plant parts (Figure 2). Any model that could be written using the matrix equation with $U = \text{NPP}$ (equation 1) would allocate the products of NPP and not GPP, independent of the respiration paradigm described by Amthor (2000).

In the following section, we look with more detail at the structure of some particular models with the aim of exploring the main source of carbon used for respiration and allocation.

105 **2.2 Representation of C allocation in models**

We reviewed the mathematical structure of 18 ecosystem models, with particular attention to the functions implemented for respiration and carbon allocation. We found that half of the models (nine) calculate a net carbon gain by subtracting both growth and maintenance respiration from GPP. In this group, maintenance respiration is generally computed based on the stock of carbon or nitrogen in vegetation pools, but it is often the case that the source of the respired carbon is the GPP flux
110 and not the carbon stored. These models include ISAM (Masri et al., 2013), IBIS (Foley et al., 1996), CTEM (Arora and Boer, 2005), HAVANA (Haverd et al., 2016), JeDi-DGVM (Pavlick et al., 2013), and the model proposed by Trugman et al. (2018). In ACONITE (Thomas and Williams, 2014), there is a maintenance respiration compartment that receives C from the labile and bud (a pool that stores C before allocation) C compartments, but not from the leaves, wood and roots. In the model proposed by Murty and McMurtrie (2000) there are different maintenance respiration terms that are subtracted from
115 GPP before allocation, only respiration from the sapwood pool depends on its C stock, while other respiration terms depend on the N stock. In FOREST-BGC (Running and Coughlan, 1988), growth respiration and available C are calculated yearly, while maintenance respiration is calculated daily from the C stocks, but both respiration variables are subtracted from GPP.

The other nine models do not consider an explicit calculation of stock-dependent maintenance respiration, and also allocate carbon from NPP. Some of these models explicitly claim that given the linear relationship between C canopy respiration and
120 canopy photosynthesis, the autotrophic respiration is a fixed fraction of the total photosynthetic fixation. Some models that fall into this category are CABLE (Wang et al., 2010), G'DAY (Comins and McMurtrie, 1993), DALEC (Williams et al., 2005), CASA (Potter et al., 1993), and TECO (Luo et al., 2012). Other models, such as the one proposed by Hilbert and Reynolds (1991) calculate the net C gain by subtracting dark respiration from GPP. Three other models do not mention respiration at all, and just partition C from a "rate of biomass production": CEVSA2 (Gu et al., 2010), the model proposed by King (1993), and
125 the model proposed by DeAngelis et al. (2012) whose net carbon production depends on leaf C.

In many models, GPP and Ra occur at short timescales (half-hourly, hourly, or daily), computing the net carbon gain as an annual integral. Carbon allocation occurs at annual intervals, when the assimilated carbon that is not respired is assigned

to a particular vegetation compartment. Therefore, the carbon that is respired at an intra-annual timescale never enters the vegetation pools.

130   The important point that we want to highlight here is that even though some models compute maintenance respiration based on knowledge of the carbon stock that needs to be maintained, this respiration is actually subtracted from GPP to obtain the net carbon gain that is subsequently allocated. Only in a few models, maintenance respiration is subtracted from a carbon stock such as a labile pool or other vegetation compartment, but most models can be written in the form of equation (1) with $U(t) = \mathrm{NPP}(t)$.

2.3   Continuous- versus discrete-time implementations

In addition to the issue of the source of carbon (GPP or NPP) used for allocation, there is a related problem in computing the age of Ra that emerges in model implementations that are discrete in time. Models based on ordinary differential equations such as those expressed as in equation (1) treat time as a continuous variable, but many models are implemented in discrete time steps where the carbon stocks of the previous time step are updated based on the functions defined by the model.

140   For example, in the Allometrically Constrained Growth and Carbon Allocation model (ACGCA, Ogle and Pacala (2009)) maintenance respiration is released from a transient non-structural carbon (NSC) pool. The carbon there is used for allocation to labile pools, structural tissue in the tree organs, and for respiration. It is a transient pool because the carbon is used immediately, which allows freshly assimilated carbon to be used for maintenance respiration. There are no issues with this implementation in continuous-time (Herrera-Ramírez et al., 2020), but in discrete-time implementations, at a one-year time-step in particular,

145   a large portion of the carbon from the transient pool never enters the tree. The net carbon balance is still correct, but the model does not describe accurately the temporal dynamics of the carbon in the transient pool.

To compute maintenance respiration in this model, carbon can be used immediately and hence never enters the tree. Growth respiration on the other hand, happens at the same time step as carbon is allocated to the tree organs but with a one year time lag, one time step after it entered the transient pool from photosynthesis. Practically, this means that growth respiration happens

150   one year later than maintenance respiration, and that carbon respired by maintenance has an age of zero. This age of respired carbon is not realistic when compared with measurements, which can be obtained at finer temporal resolutions and over a broader range.

3   Age of respired carbon obtained as the transit time distribution from models

The age of respired carbon can be obtained from ecosystem models, but the model structure and the form in which the source

155   of carbon for allocation is represented has an impact on the age of carbon respired from ecosystems. Although most models do not represent carbon age explicitly, it can be computed using different computational approaches.

The age of respired carbon from ecosystem is characterized by its transit time distribution (Bolin and Rodhe, 1973; Thompson and Randerson, 1999; Sierra et al., 2021b). These distributions can be obtained from ecosystem carbon models using impulse response functions (Thompson and Randerson, 1999), a simulation approach that consists of applying a pulse of car-

160 bon to a model at equilibrium, where carbon stocks do not change over time, and then observing the respiration flux after
the pulse. These distributions can also be obtained using the analytical formulas developed by Metzler and Sierra (2018) for
models at equilibrium, or the approach described in Metzler et al. (2018) for models out of equilibrium.

The transit time distribution represents the proportions of respired carbon that have different ages, and it is usually a contin-
uous function that results from a mixture of exponential functions (Metzler and Sierra, 2018). They can be obtained from any

165 ecosystem model expressed in compartmental form as

$$\frac{\mathrm{d}\boldsymbol{x}}{\mathrm{d}t} = \boldsymbol{u}(t) + \mathbf{B}(t)\,\boldsymbol{x} \tag{2}$$

where $\boldsymbol{u}(t)$ is a vector of carbon inputs to the system. In the framework of Luo et al. (2017), $\boldsymbol{u}(t) = U(t)\,\boldsymbol{b}$. The matrix $\mathbf{B}$ is a
compartmental matrix with diagonal elements the cycling rates within the pools, and off-diagonal elements the transfer rates of
carbon among the different pools. In the framework of Luo et al. (2017), $\mathbf{B}(t) = \xi(t)\mathbf{A}\,\mathbf{K}$. Respiration from each compartment

170 j can be obtained as the product of the amount of mass present in the system and a rate of release z_j,

$$r_j = z_j\,x_j. \tag{3}$$

This rate of release z can be obtained from the compartmental matrix $\mathbf{B}$ as the sum of the entries of each column. It represents
the fraction of carbon that leaves each pool and is not transferred to any other pool.

The transit time distribution of carbon can be defined as the age of the respired carbon from the pools, and can be expressed

175 as (Metzler and Sierra, 2018)

$$f_T(\tau) = \frac{1}{\|\boldsymbol{r}\|}\sum_j r_j f_{aj}(\tau) = \frac{1}{\|\boldsymbol{r}\|}\sum_j z_j\,x_j f_{aj}(\tau), \tag{4}$$

where $f_{aj}(\tau)$ is the age distribution function for pool j as a function of the variable τ which represents age. The norm symbol
$\|\ \|$ represents the sum of all elements of the vector.

If carbon is allocated from GPP, i.e. $\boldsymbol{u}(t) = \mathrm{GPP}(t)\,\boldsymbol{b}(t)$, autotrophic respiration can only occur directly from the carbon

180 stored in the pools, and $z_j > 0$ for all pools (Figure 2a). Conversely, if carbon is allocated from NPP, i.e. $\boldsymbol{u}(t) = (\mathrm{GPP}(t) -
\mathrm{Ra}(t))\,\boldsymbol{b}(t)$, no respiration occurs from vegetation pools and $z_j = 0$ for those pools (Figure 2b). We can infer then from
equation (4) that for those pools that do not respire carbon ($z_j = r_j = 0$), their contribution to the transit time distribution is
equal to zero.

For illustration purposes, we will show here predictions from the global carbon model developed by Emanuel et al. (1981)

185 and used by Thompson and Randerson (1999) to represent differences between carbon allocation from GPP versus allocation
from NPP. We will refer to these two cases as GPP-based versus NPP-based carbon allocation schemes.

At equilibrium, the GPP-based version of the model shows a continuous distribution of carbon that decreases with transit
time (Figure 3). A large proportion of carbon is respired very quickly after photosynthetic fixation and smaller quantities are
respired later on. In contrast, the NPP-based version of the model predicts that all autotrophically respired carbon has an age of

190 zero, and respiration in later years comes only from heterotrophic pools. The median age of the respired carbon (50% quantile
of the transit time distribution) in the GPP-based version of the model is 2.3 yr, i.e. 50 % of respired carbon is respired in
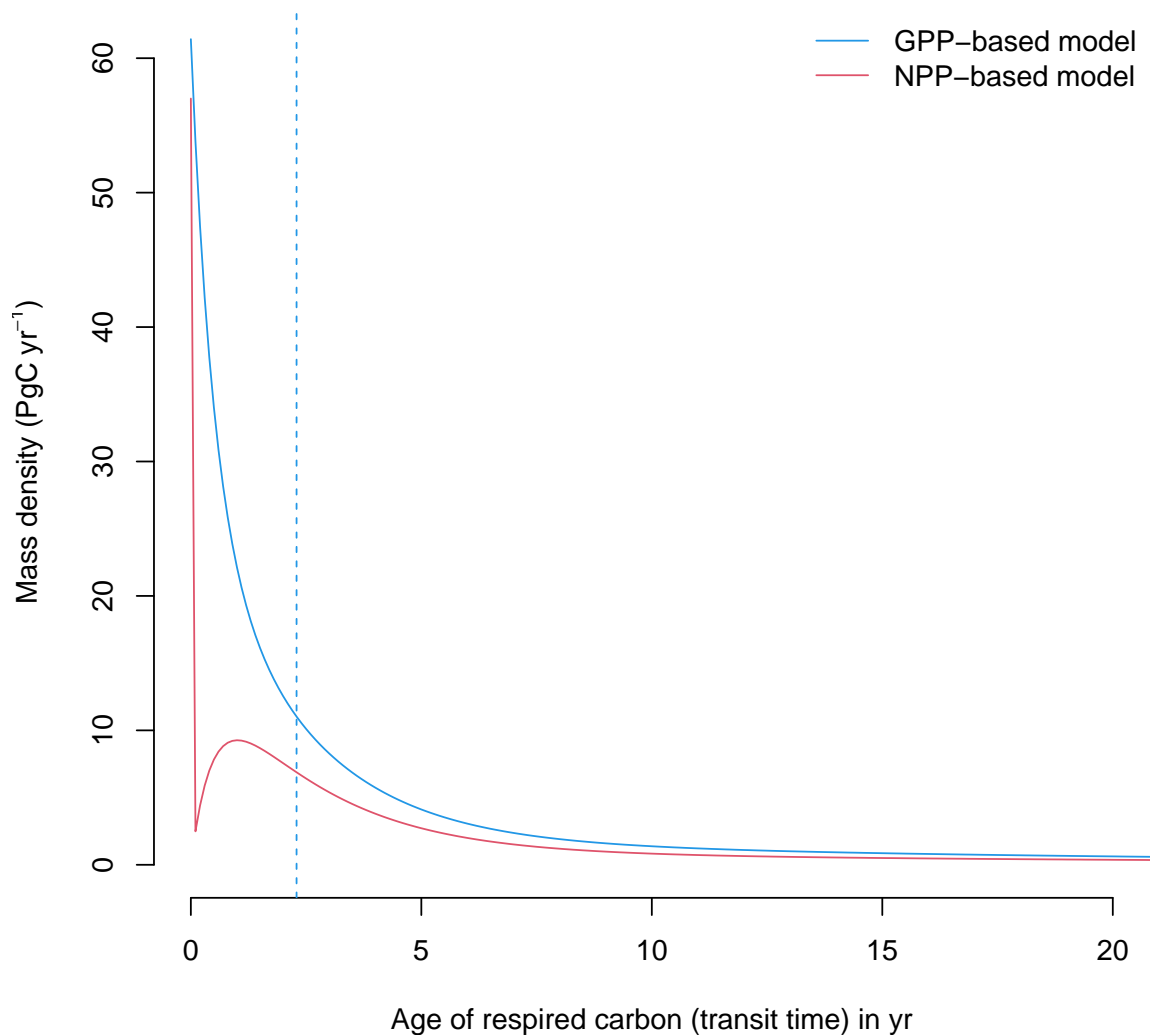
Figure 3. Transit time distributions obtained from the GPP- and the NPP-based versions of the model of Emanuel et al. (1981). The vertical dashed line represents the median transit time of the GPP-based model, which is 2.3 yr. For the NPP-version, the median transit time is 0 yr.

less than 2.3 years. In contrast, in the NPP-based version of the model the median transit time is 0 yr, because the autotrophic respiration flux, which corresponds to 50 % of GPP, is removed immediately after photosynthetic fixation.
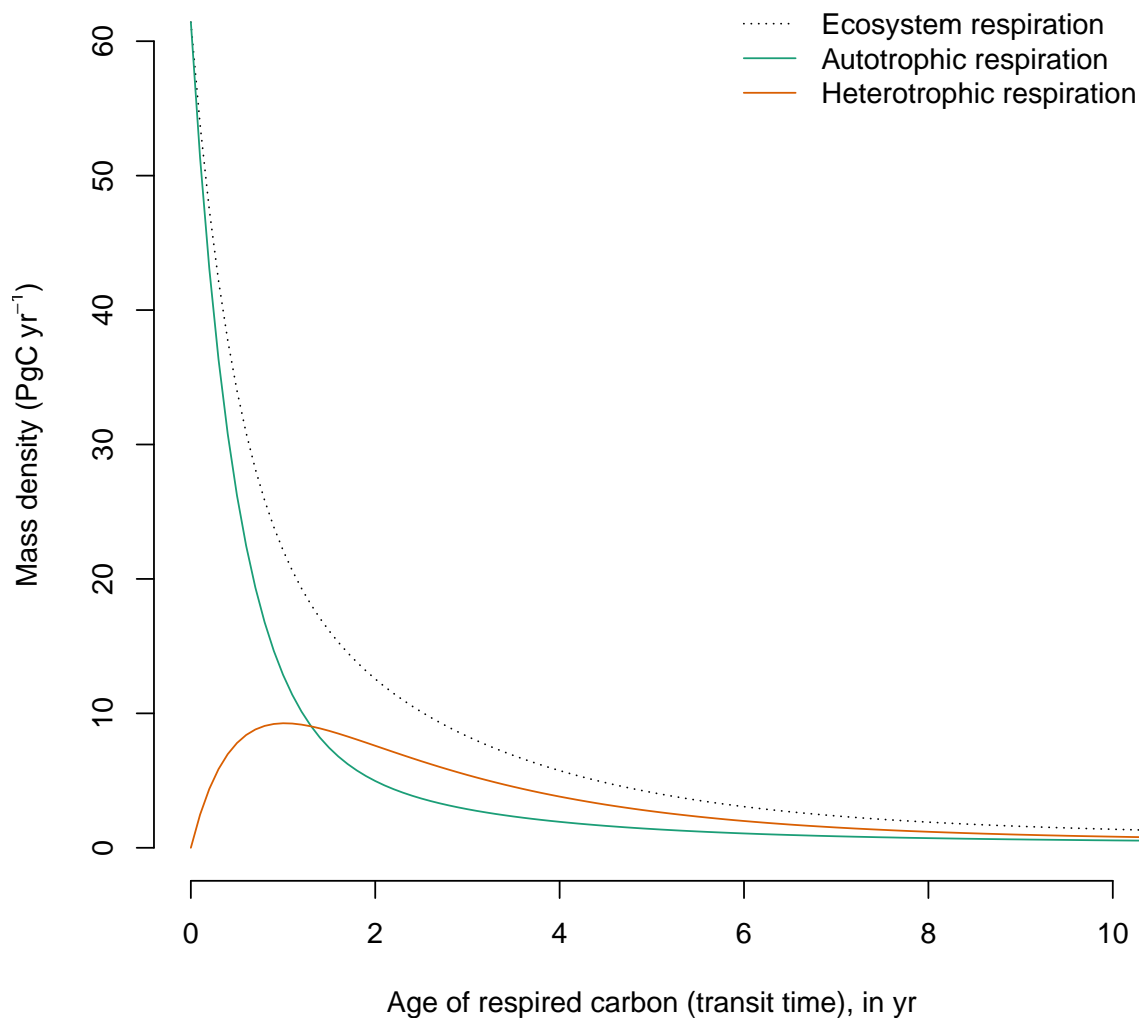
Figure 4. Contribution of autotrophic and heterotrophic respiration to the transit time distribution in the GPP-based version of the model of Emanuel et al. (1981). The age distribution of total ecosystem respiration is equivalent to the transit time distribution of the ecosystem.

The GPP-based version of the model predicts a continuum of ages of respired carbon both for autotrophic and heterotrophic
195   respiration (Figure 4). Although a large portion of autotrophic respiration is very young (< 1 year), a significant proportion is older and can be respired years after photosynthetic fixation.

4 Age of respired carbon obtained from radiocarbon measurements

Several studies have used radiocarbon-based methods to estimate the age of the respired carbon form different compartments of the ecosystem (e.g., foliage, wood, roots, and soil) (Carbone and Trumbore, 2007; Carbone et al., 2007, 2013; Muhr et al., 2013, 2018; Trumbore et al., 2015). In vegetation compartments, studies have focused mostly on individual trees rather than on a larger sample of trees within a forest stand. For healthy mature trees, small differences have been found between compartments, for example carbon respired from leaves may be less than one year old (Carbone and Trumbore, 2007), while in roots and stems the respired carbon is on average older than one year, with a mix of carbon from recent assimilates and some contributions of old carbon from storage reserves (Muhr et al., 2018). There is empirical evidence that shows that the age of the respired carbon by trees can change during different seasons, and increases as trees are exposed to stress and have to use their storage reserves to support metabolic activity. For instance, Carbone et al. (2013) reported ages of the respired CO_2 by the stem of *Acer rubrum* trees of 1.5 and $\sim$0 yr during spring and late summer, respectively. Muhr et al. (2013) reported ages of 2.5 and 3.3 yr for CO_2 respired from the stem of *Simaruba amara* trees during the dry and the wet season, respectively; 2 years old CO_2 from the stem of *Tachigali paniculata*; and 4.5 and 4 yr old CO_2 from stems of *Hymenolobium pulcherrimum*. Herrera et al (in prep) found similar values as in these previous studies, 5 and 3 years old for CO_2 respired by in-stem samples of *Dacriodes microcarpa*, and 2.5 and 5 years old for CO_2 from *Ocotea leucoxylon* during the dry and wet season, respectively. Some studies have also reported several years old respired CO_2, ranging from 1 to 5 yr from roots. Most of these studies report mean values of 4 yr old respired carbon from roots (Czimczik et al., 2006; Schuur and Trumbore, 2006; Carbone and Trumbore, 2007), but younger CO_2 (0.6 yr old) has been also reported by Hilman et al. (2021).

Physical damage such as girdling increases the age of the respired CO_2. For example, Muhr et al. (2018) reported 1 year old CO_2 respired by healthy *Scleronema micranthum* trees and 14 years old CO_2 respired by trees after one year of girdling. Also, Hilman et al. (2021) reported increases in the age of the respired carbon from roots, ranging from 0.6 yr from not girdled trees to 1.3 yr for girdled tress after 1 year.

With very few exceptions, most of the empirical evidence supports the idea that respired carbon from vegetation parts is on average older than 1 yr, but higher values can be observed depending on the season or on whether trees suffer some form of physiological stress that decreases the supply of recent carbohydrates (Herrera-Ramírez et al., 2020).

This empirical evidence, which shows that the age of respired carbon spans from one to several years (Figure 5), is inconsistent with predictions from models in which carbon allocation is based on NPP where the age of respired carbon is exactly equal to zero (Figure 3).

5 Implications

The modeling choice of allocating carbon from NPP and not from GPP has important consequences for: (1) use of radiocarbon as an empirical constraint in model-data assimilation studies; (2) computing the transit time distribution of carbon in ecosystems; and (3) determining isotopic exchange between terrestrial ecosystems and the atmosphere. We briefly elaborate on these three implications in the following paragraphs.
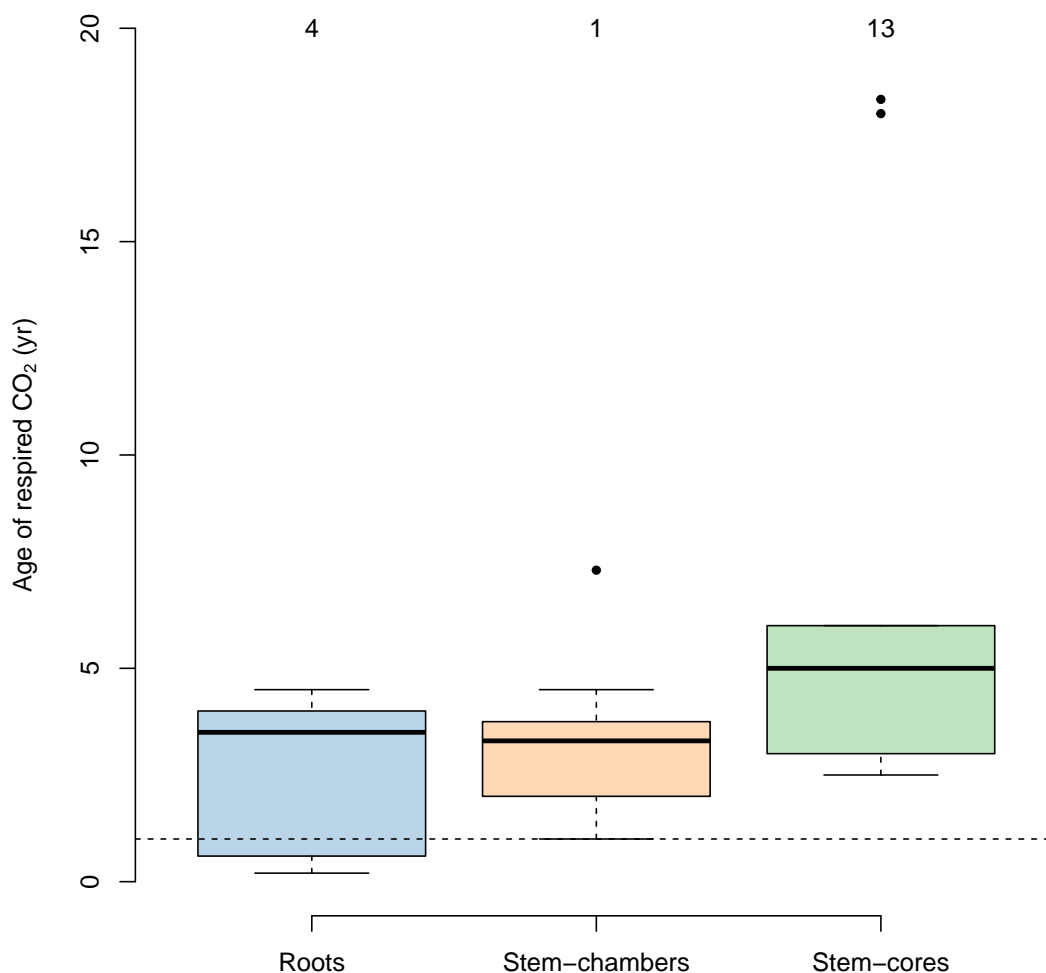
Figure 5. Age of C in respired CO_2 from roots and stems for different tree species from temperate and tropical forests obtained from radiocarbon measurements. Data for roots include both fine and coarse roots, and data for stems is split between chamber based measurements and incubations of tree cores. Numbers on top of the boxes represent the number of observations available to draw the boxplots. Values below the horizontal dashed line represent measurements of carbon younger than 1 yr.

230   First, as radiocarbon measurements become increasingly available for plant parts and respired CO_2 from ecosystems, there is an excellent opportunity to use these data for constraining vegetation models and testing model-based hypotheses. Model-data assimilation techniques are very powerful to reduce model structural uncertainty, and can be used to improve carbon allocation and respiration routines in models. However, as we have shown here, the age of respired CO_2 in NPP-based models

is predicted as exactly zero, inconsistent with radiocarbon measurements. Therefore, by construction, NPP-based allocation

235 schemes cannot be used to assimilate radiocarbon measurements and constrain allocation and respiration functions.

Second, under the assumption of equilibrium, mean transit times of carbon in ecosystems can be obtained by dividing the total carbon stock over the total input flux. However, this approach provides no information on its underlying probability distribution. As shown above, the median transit time can deviate strongly from the mean, and the possibility to compute entire transit time distributions provides very useful information to integrate processes occurring at very different timescales (Sierra

240 et al., 2021b). Models that subtract autotrophic respiration from GPP before allocating to plant parts cannot be used to compute entire transit time distributions, missing on an opportunity to improve our understanding of the timescales of carbon exchange between ecosystems and the atmosphere.

Third, the choice of allocation scheme also has consequences for predicting the isotopic exchange of carbon between ecosystems and the atmosphere. For instance, predictions of radiocarbon signatures of respired CO_2 from the terrestrial biosphere

245 show a large difference between the GPP- and NPP-based versions of the simple model (Figure 6). Because carbon spends less time in NPP-based allocation schemes, the isotopic exchange between plant parts and the atmosphere occurs more rapidly than in the GPP-based representations. These differences may have important implications for predicting the isotopic disequilibrium between carbon reservoirs at the Earth system level (Randerson et al., 2002; Levin et al., 2021).

6 Summary and recommendations

250 We have shown that models in which carbon allocation occurs after autotrophic respiration is subtracted from GPP (i.e. NPP-based models) predict that the age of respired carbon from vegetation pools is zero. This prediction contradicts empirical evidence based on the isotopic signature of respired CO_2 from plant parts, and suggests that GPP-based allocation schemes are more appropriate to represent carbon allocation and respiration in models. Models in which allocation is based on NPP miss on the opportunity to use radiocarbon data for constraining model parameters and improve their representation of vegetation

255 processes. They are also unable to produce realistic transit time distributions of carbon, and can provide misleading predictions of isotopic exchange between ecosystems and the atmosphere.

We recommend modeling teams to revise the functions used to compute autotrophic respiration in models, in particular allowing carbon to enter into vegetation pools and then subtracting the autotrophic respiration flux from the standing carbon stock. The addition of a non-structural carbohydrate pool can help to improve the dynamics of active carbon that is used to

260 maintain metabolic processes (Herrera-Ramírez et al., 2020), but models must ensure that the respired carbon is removed from these NSC pools and not from GPP. Also, care must be taken in avoiding artifacts introduced by the time step of the model in discrete-time implementations that may introduce time lags in the use of carbon for respiration.

Radiocarbon measurements in respired CO_2 from plant parts and whole ecosystem pools can greatly help to test the mathematical structure of autotrophic respiration and allocation functions in models. These measurements are only available for a

265 small set of sites, but future efforts should expand to more diverse ecosystems, capturing patterns induced by environmental
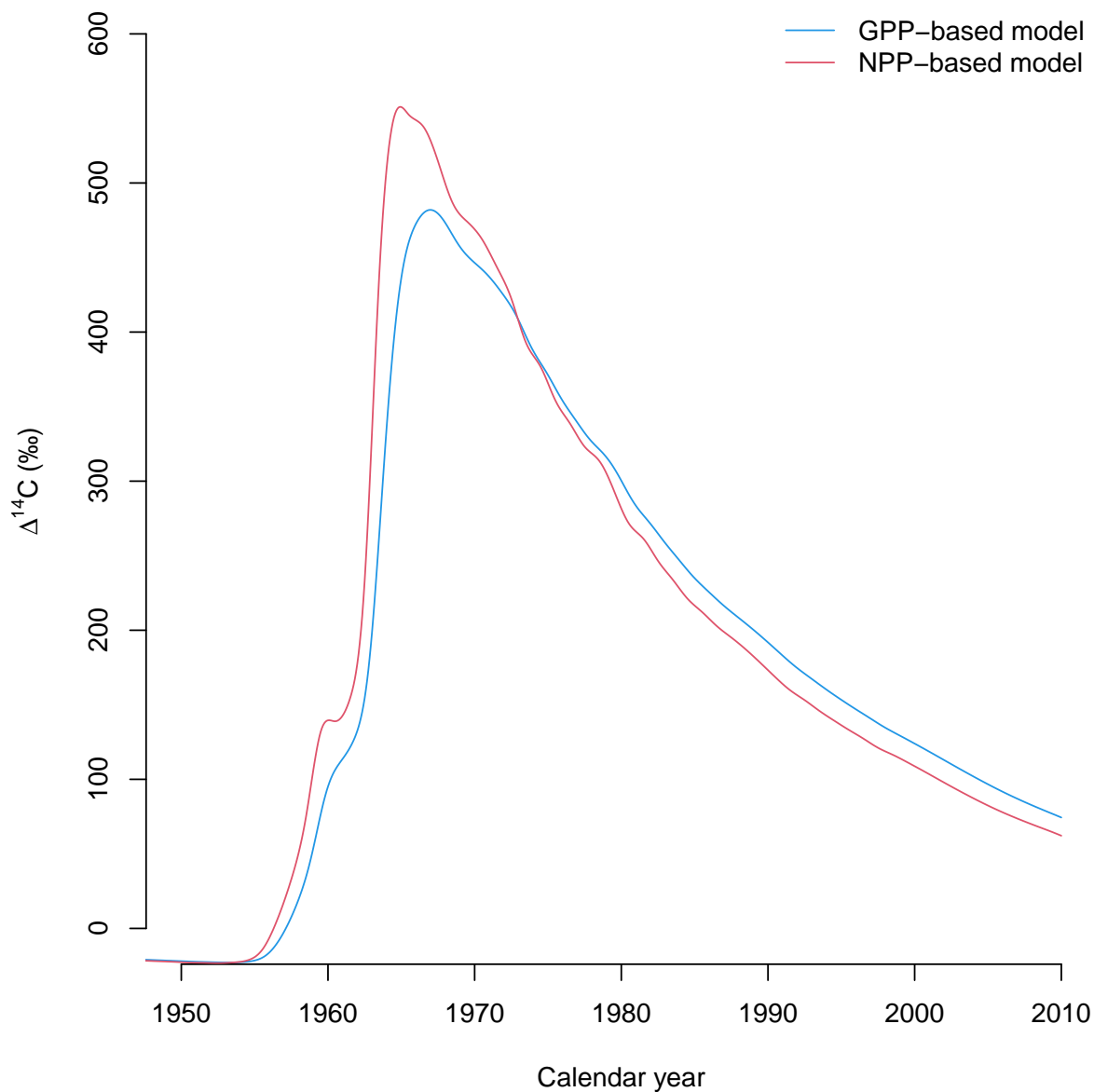
Figure 6. Radiocarbon in respired CO_2 (in $\Delta^{14}C$) predicted by the two versions of the simple model of Emanuel et al. (1981). The version in which carbon allocation occurs after Ra is subtracted from GPP (NPP-based model) predicts a faster exchange of radiocarbon with the atmosphere than the GPP-based version of the model where carbon stays for a longer time in the ecosystem.

drivers. Assimilation of radiocarbon data into ecosystem models offers large opportunities to improve our overall understanding of the timescales of carbon cycling in ecosystems and how they respond to environmental change.

Code and data availability. All data and code used for this manuscript is available at https://github.com/crlsierra/allocationGPPorNPP. Upon acceptance, a static copy of the repository will be archived in Zenodo and will be cited with a doi.

270 *Author contributions.* CAS designed research and wrote the manuscript. DHR compiled empirical studies on radiocarbon. VCN reviewed literature on models. HM analyzed differences between discrete and continuous implementations of Ra in models. HH wrote sections on physiology. All authors discussed ideas and contributed to writing.

Competing interests. The authors declare no competing interests.

Acknowledgements. Funding was provided by the German Research Foundation (SI 1953/2-2), the Max Planck Society, and the Swedish
275 University for Agricultural Sciences. HM acknowledges the support of the Swedish Research Council for Sustainable Development FOR-MAS, under grant 2018-01820.

References

Amthor, J. S.: The McCree-de Wit-Penning de Vries-Thornley Respiration Paradigms: 30 Years Later, Ann Bot, 86, 1–20, 2000.

Arora, V. K. and Boer, G. J.: A parameterization of leaf phenology for the terrestrial ecosystem component of climate models, Global Change Biology, 11, 39–59, https://doi.org/10.1111/j.1365-2486.2004.00890.x, 2005.

Bolin, B. and Rodhe, H.: A note on the concepts of age distribution and transit time in natural reservoirs, Tellus, 25, 58–62, 1973.

Carbone, M. S. and Trumbore, S. E.: Contribution of new photosynthetic assimilates to respiration by perennial grasses and shrubs: residence times and allocation patterns, New Phytologist, 176, 124–135, https://doi.org/https://doi.org/10.1111/j.1469-8137.2007.02153.x, 2007.

Carbone, M. S., Czimczik, C. I., McDuffee, K. E., and Trumbore, S. E.: Allocation and residence time of photosynthetic products in a boreal forest using a low-level 14C pulse-chase labeling technique, Global Change Biology, 13, 466–477, https://doi.org/https://doi.org/10.1111/j.1365-2486.2006.01300.x, 2007.

Carbone, M. S., Czimczik, C. I., Keenan, T. F., Murakami, P. F., Pederson, N., Schaberg, P. G., Xu, X., and Richardson, A. D.: Age, allocation and availability of nonstructural carbon in mature red maple trees, New Phytologist, 200, 1145–1155, https://doi.org/https://doi.org/10.1111/nph.12448, 2013.

Ceballos-Núñez, V., Müller, M., and Sierra, C. A.: Towards better representations of carbon allocation in vegetation: a conceptual framework and mathematical tool, Theoretical Ecology, 13, 317–332, https://doi.org/10.1007/s12080-020-00455-w, 2020.

Collalti, A. and Prentice, I. C.: Is NPP proportional to GPP? Waring's hypothesis 20 years on, Tree Physiology, 39, 1473–1483, https://doi.org/10.1093/treephys/tpz034, 2019.

Comins, H. N. and McMurtrie, R. E.: Long-Term Response of Nutrient-Limited Forests to CO_2 Enrichment; Equilibrium Behavior of Plant-Soil Models, Ecological Applications, 3, 666–681, http://www.jstor.org/stable/1942099, 1993.

Czimczik, C., C. I., Trumbore, S. E., Carbone, M. S., and Winston, G. C.: Changing sources of soil respiration with time since fire in a boreal forest, Global Change Biology, 12, 957–971, https://doi.org/https://doi.org/10.1111/j.1365-2486.2006.01107.x, 2006.

DeAngelis, D., Ju, S., Liu, R., Bryant, J., and Gourley, S.: Plant allocation of carbon to defense as a function of herbivory, light and nutrient availability, Theoretical Ecology, 5, 445–456, https://doi.org/10.1007/s12080-011-0135-z, 2012.

DeLucia, E. H., Drake, J. E., Thomas, R. B., and Gonzalez-Meler, M.: Forest carbon use efficiency: is respiration a constant fraction of gross primary production?, Global Change Biology, 13, 1157–1167, https://doi.org/10.1111/j.1365-2486.2007.01365.x, 2007.

Emanuel, W. R., Killough, G. G., and Olson, J. S.: Modelling the circulation of carbon in the world's terrestrial ecosystems, in: Carbon Cycle Modelling, edited by Bolin, B., SCOPE 16, pp. 335–353, John Wiley and Sons, 1981.

Foley, J. A., Prentice, I. C., Ramankutty, N., Levis, S., Pollard, D., Sitch, S., and Haxeltine, A.: An integrated biosphere model of land surface processes, terrestrial carbon balance, and vegetation dynamics, Global Biogeochemical Cycles, 10, 603–628, https://doi.org/10.1029/96GB02692, 1996.

Franklin, O., Johansson, J., Dewar, R. C., Dieckmann, U., McMurtrie, R. E., Brännström, Å., and Dybzinski, R.: Modeling carbon allocation in trees: a search for principles, Tree Physiology, 32, 648–666, https://doi.org/10.1093/treephys/tpr138, 2012.

Gu, F., Zhang, Y., Tao, B., Wang, Q., and Yu, G.: Modeling the effects of nitrogen deposition on carbon budget in two temperate forests, Ecological complexity, 7, 139–148, https://doi.org/10.1016/j.ecocom.2010.04.002, 2010.

Hagedorn, F., Joseph, J., Peter, M., Luster, J., Pritsch, K., Geppert, U., Kerner, R., Molinier, V., Egli, S., Schaub, M., Liu, J.-F., Li, M., Sever, K., Weiler, M., Siegwolf, R. T. W., Gessler, A., and Arend, M.: Recovery of trees from drought depends on belowground sink control, Nature Plants, 2, 16 111, https://doi.org/10.1038/nplants.2016.111, 2016.

Hartmann, H. and Trumbore, S.: Understanding the roles of nonstructural carbohydrates in forest trees – from what we can measure to what
315   we want to know, New Phytologist, 211, 386–403, https://doi.org/10.1111/nph.13955, 2016-21190, 2016.

Haverd, V., Smith, B., Raupach, M., Briggs, P., Nieradzik, L., Beringer, J., Hutley, L., Trudinger, C. M., and Cleverly, J.: Coupling carbon
allocation with leaf and root phenology predicts tree–grass partitioning along a savanna rainfall gradient, Biogeosciences, 13, 761–779,
https://doi.org/10.5194/bg-13-761-2016, 2016.

Herrera-Ramírez, D., Muhr, J., Hartmann, H., Römermann, C., Trumbore, S., and Sierra, C. A.: Probability distributions of nonstruc-
320   tural carbon ages and transit times provide insights into carbon allocation dynamics of mature trees, New Phytologist, 226, 1299–1311,
https://doi.org/10.1111/nph.16461, 2020.

Hilbert, D. W. and Reynolds, J. F.: A Model Allocating Growth Among Leaf Proteins, Shoot Structure, and Root Biomass to Produce
Balanced Activity, Annals of Botany, 68, 417–425, http://aob.oxfordjournals.org/content/68/5/417.abstract, 1991.

Hilman, B., Muhr, J., Helm, J., Kuhlmann, I., Schulze, E.-D., and Trumbore, S.: The size and the age of the metabolically active carbon in
325   tree roots, Plant, Cell & Environment, 44, 2522–2535, https://doi.org/https://doi.org/10.1111/pce.14124, 2021.

Huang, J., Forkelová, L., Unsicker, S. B., Forkel, M., Griffith, D. W., Trumbore, S., and Hartmann, H.: Isotope labeling reveals contribution
of newly fixed carbon to carbon storage and monoterpenes production under water deficit and carbon limitation, Environmental and
Experimental Botany, 162, 333–344, https://doi.org/https://doi.org/10.1016/j.envexpbot.2019.03.010, 2019a.

Huang, J., Hammerbacher, A., Weinhold, A., Reichelt, M., Gleixner, G., Behrendt, T., van Dam, N. M., Sala, A., Gershenzon, J., Trumbore, S.,
330   and Hartmann, H.: Eyes on the future – evidence for trade-offs between growth, storage and defense in Norway spruce, New Phytologist,
222, 144–158, https://doi.org/https://doi.org/10.1111/nph.15522, 2019b.

King, D. A.: A model analysis of the influence of root and foliage allocation on forest production and competition between trees, Tree
Physiology, 12, 119–135, https://doi.org/10.1093/treephys/12.2.119, 1993.

Levin, I., Hammer, S., Kromer, B., Preunkert, S., Weller, R., and Worthy, D. E.: Radiocarbon in global tropospheric carbon dioxide, Radio-
335   carbon, pp. 1–11, https://doi.org/10.1017/RDC.2021.102, 2021.

Litton, C. M., Raich, J. W., and Ryan, M. G.: Carbon allocation in forest ecosystems, Global Change Biology, 13, 2089–2109, 2007.

Lu, X., Wang, Y.-P., Luo, Y., and Jiang, L.: Ecosystem carbon transit versus turnover times in response to climate warming and rising
atmospheric CO_2 concentration, Biogeosciences, 15, 6559–6572, https://doi.org/10.5194/bg-15-6559-2018, 2018.

Luo, Y., Weng, E., and Yang, Y.: Ecosystem Ecology, in: Encyclopedia of Theoretical Ecology, edited by Hastings, A. and Gross, L., pp.
340   219–229, University of California Press, Berkeley, 2012.

Luo, Y., Shi, Z., Lu, X., Xia, J., Liang, J., Jiang, J., Wang, Y., Smith, M. J., Jiang, L., Ahlström, A., Chen, B., Hararuk, O., Hastings, A.,
Hoffman, F., Medlyn, B., Niu, S., Rasmussen, M., Todd-Brown, K., and Wang, Y.-P.: Transient dynamics of terrestrial carbon storage:
mathematical foundation and its applications, Biogeosciences, 14, 145–161, https://doi.org/10.5194/bg-14-145-2017, 2017.

Malhi, Y., Doughty, C., and Galbraith, D.: The allocation of ecosystem net primary productivity in tropical forests, Philosophical Transactions
345   of the Royal Society B: Biological Sciences, 366, 3225–3245, 2011.

Malhi, Y., Doughty, C. E., Goldsmith, G. R., Metcalfe, D. B., Girardin, C. A. J., Marthews, T. R., del Aguila-Pasquel, J., Aragão, L. E. O. C.,
Araujo-Murakami, A., Brando, P., da Costa, A. C. L., Silva-Espejo, J. E., Farfán Amézquita, F., Galbraith, D. R., Quesada, C. A., Rocha,
W., Salinas-Revilla, N., Silvério, D., Meir, P., and Phillips, O. L.: The linkages between photosynthesis, productivity, growth and biomass
in lowland Amazonian forests, Global Change Biology, 21, 2283–2295, https://doi.org/10.1111/gcb.12859, 2015.

350   Masri, B. E., Barman, R., Meiyappan, P., Song, Y., and Liang, M.: Carbon dynamics in the Amazonian Basin: Integration of
        eddy covariance and ecophysiological data with a land surface model, Agricultural and forest meteorology, 182, 156–167,
        https://doi.org/10.1016/j.agrformet.2013.03.011, 2013.

      Metzler, H. and Sierra, C. A.: Linear Autonomous Compartmental Models as Continuous-Time Markov Chains: Transit-Time and Age
        Distributions, Mathematical Geosciences, 50, 1–34, https://doi.org/10.1007/s11004-017-9690-1, 2018.

355   Metzler, H., Müller, M., and Sierra, C. A.: Transit-time and age distributions for nonlinear time-dependent compartmental systems, Proceed-
        ings of the National Academy of Sciences, 115, 1150–1155, https://doi.org/10.1073/pnas.1705296115, 2018.

      Muhr, J., Angert, A., Negrón-Juárez, R. I., Muñoz, W. A., Kraemer, G., Chambers, J. Q., and Trumbore, S. E.: Carbon dioxide emitted from
        live stems of tropical trees is several years old, Tree Physiology, 33, 743–752, https://doi.org/10.1093/treephys/tpt049, 2013.

      Muhr, J., Trumbore, S., Higuchi, N., and Kunert, N.: Living on borrowed time – Amazonian trees use decade-old storage carbon to survive
360   for months after complete stem girdling, New Phytologist, 220, 111–120, https://doi.org/https://doi.org/10.1111/nph.15302, 2018.

      Murty, D. and McMurtrie, R.: The decline of forest productivity as stands age: A model-based method for analysing causes for the decline,
        Ecological modelling, 134, 185–205, https://doi.org/10.1016/S0304-3800(00)00345-8, 2000.

      Neubauer, S. C. and Megonigal, J. P.: Moving Beyond Global Warming Potentials to Quantify the Climatic Role of Ecosystems, Ecosystems,
        18, 1000–1013, https://doi.org/10.1007/s10021-015-9879-4, 2015.

365   Ogle, K. and Pacala, S. W.: A modeling framework for inferring tree growth and allocation from physiological, morphological and allometric
        traits, Tree Physiology, 29, 587–605, https://doi.org/10.1093/treephys/tpn051, 2009.

      Pavlick, R., Drewry, D. T., Bohn, K., Reu, B., and Kleidon, A.: The Jena Diversity-Dynamic Global Vegetation Model (JeDi-DGVM): a
        diverse approach to representing terrestrial biogeography and biogeochemistry based on plant functional trade-offs, Biogeosciences, 10,
        4137–4177, https://doi.org/10.5194/bg-10-4137-2013, 2013.

370   Potter, C. S., Randerson, J. T., Field, C. B., Matson, P. A., Vitousek, P. M., Mooney, H. A., and Klooster, S. A.: Terrestrial
        ecosystem production: A process model based on global satellite and surface data, Global Biogeochemical Cycles, 7, 811–841,
        https://doi.org/10.1029/93GB02725, 1993.

      Randerson, J. T., Enting, I. G., Schuur, E. A. G., Caldeira, K., and Fung, I. Y.: Seasonal and latitudinal variability of troposphere $\Delta^{14}CO_2$:
        Post bomb contributions from fossil fuels, oceans, the stratosphere, and the terrestrial biosphere, Global Biogeochemical Cycles, 16,
375   59–1–59–19, https://doi.org/10.1029/2002GB001876, 2002.

      Rasmussen, M., Hastings, A., Smith, M. J., Agusto, F. B., Chen-Charpentier, B. M., Hoffman, F. M., Jiang, J., Todd-Brown, K. E. O.,
        Wang, Y., Wang, Y.-P., and Luo, Y.: Transit times and mean ages for nonautonomous and autonomous compartmental systems, Journal of
        Mathematical Biology, 73, 1379–1398, https://doi.org/10.1007/s00285-016-0990-8, 2016.

      Running, S. W. and Coughlan, J. C.: A general model of forest ecosystem processes for regional applications I. Hydrologic balance, canopy
380   gas exchange and primary production processes, Ecological Modelling, 42, 125–154, https://doi.org/http://dx.doi.org/10.1016/0304-
        3800(88)90112-3, 1988.

      Schuur, E. A. G. and Trumbore, S. E.: Partitioning sources of soil respiration in boreal black spruce forest using radiocarbon, Global Change
        Biology, 12, 165–176, https://doi.org/https://doi.org/10.1111/j.1365-2486.2005.01066.x, 2006.

      Sierra, C. A., Crow, S. E., Heimann, M., Metzler, H., and Schulze, E.-D.: The climate benefit of carbon sequestration, Biogeosciences, 18,
385   1029–1048, https://doi.org/10.5194/bg-18-1029-2021, 2021a.

      Sierra, C. A., Estupinan-Suarez, L. M., and Chanca, I.: The fate and transit time of carbon in a tropical forest, Journal of Ecology, 109,
        2845–2855, https://doi.org/https://doi.org/10.1111/1365-2745.13723, 2021b.

Thomas, R. Q. and Williams, M.: A model using marginal efficiency of investment to analyze carbon and nitrogen interactions in terrestrial ecosystems (ACONITE Version 1), Geoscientific Model Development, 7, 2015–2037, https://doi.org/10.5194/gmd-7-2015-2014, 2014.

390   Thompson, M. V. and Randerson, J. T.: Impulse response functions of terrestrial carbon cycle models: method and application, Global Change Biology, 5, 371–394, 10.1046/j.1365-2486.1999.00235.x, 1999.

Trugman, A. T., Detto, M., Bartlett, M. K., Medvigy, D., Anderegg, W. R. L., Schwalm, C., Schaffer, B., and Pacala, S. W.: Tree carbon allocation explains forest drought-kill and recovery patterns, Ecology Letters, 21, 1552–1560, https://doi.org/10.1111/ele.13136, 2018.

Trumbore, S.: Carbon respired by terrestrial ecosystems – recent progress and challenges, Global Change Biology, 12, 141–153,
395   https://doi.org/10.1111/j.1365-2486.2006.01067.x, 2006.

Trumbore, S., Czimczik, C. I., Sierra, C. A., Muhr, J., and Xu, X.: Non-structural carbon dynamics and allocation relate to growth rate and leaf habit in California oaks, Tree Physiology, 35, 1206–1222, https://doi.org/10.1093/treephys/tpv097, 2015.

Wang, Y. P., Law, R. M., and Pak, B.: A global model of carbon, nitrogen and phosphorus cycles for the terrestrial biosphere, Biogeosciences, 7, 2261–2282, https://doi.org/10.5194/bg-7-2261-2010, 2010.

400   Waring, R. H., Landsberg, J. J., and Williams, M.: Net primary production of forests: a constant fraction of gross primary production?, Tree Physiol, 18, 129–134, 1998.

Williams, M., Schwarz, P. A., Law, B. E., Irvine, J., and Kurpius, M. R.: An improved analysis of forest carbon dynamics using data assimilation, Global Change Biology, 11, 89–105, https://doi.org/10.1111/j.1365-2486.2004.00891.x, 2005.