**Allocation of carbon from Net Primary Production in models is inconsistent with observations of the age of respired carbon**

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Carbon allocation in vegetation is one of the most important processes in the terrestrial carbon cycle; it determines the fate of photo-assimilates and it has an impact on the time carbon spends in ecosystems as well as on the overall carbon balance. 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 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 allocated only after autotrophic respiration losses are subtracted from GPP. However, empirical work that estimates the age of respired CO 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 occurs briefly after fixation. 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.

# 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 due to respiration from autotrophic and heterotrophic organisms, but the time it would take this carbon to return to the atmosphere depends strongly on what plant part the carbon is allocated to (Rasmussen et al. 2016; Y. Luo et al. 2017; Lu et al. 2018; Herrera-Ramı́rez 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 where it can stay 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 (Neubauer and Megonigal 2015; C. A. Sierra et al. 2021); 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.

Although there have been important recent advances in the understanding of physiological-level mechanisms of autotrophic respiration and carbon allocation in plants (Hartmann and Trumbore 2016), the representation of these processes in land-surface and Earth system models remains overly simplistic. Many models represent autotrophic respiration as a constant proportion of gross primary production (GPP) (Figure [1](#fig:annualRaGPP)), and the remaining carbon (net primary production NPP) is allocated to different plant parts according to fixed partitioning coefficients (Franklin et al. 2012; Ceballos-Núñez, Müller, and Sierra 2020). This approach is useful to model ecosystem-level carbon balances because it simplifies the representation of autotrophic respiration as a simple ratio of GPP to carbon use efficiency. However, we argue here that for a more in depth understanding of the fate of photosynthates and the time carbon stays in ecosystems, carbon allocation functions need to be revisited in many models so to avoid predictions in conflict with empirical observations.

![Ratio of autotrophic respiration Ra to gross primary production GPP 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.](data:application/pdf;base64,)

Ratio of autotrophic respiration Ra to gross primary production GPP 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.

In this manuscript we would like to: (1) review models and conceptual frameworks on the main approaches used to represent carbon allocation at the ecosystem level; (2) show that models that allocate carbon from NPP and not from GPP predict a transit time equals to zero for the entire autotrophic respiration flux, or in other words, respired carbon from vegetation pools have an age equal to zero; (3) demonstrate that this prediction is inconsistent with measurements of the age of respired carbon obtained with radiocarbon measurements and do not capture the variability in the transit time of carbon from vegetation; (4) highlight that the choice of carbon allocation approach have consequences for predicting isotopic 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.

# Historical context and conceptual frameworks

Waring, Landsberg, and Williams (1998) proposed that net primary production (NPP) is a constant proportion of gross primary production (GPP), with a constant ratio NPP/GPP = 0.47, or Ra/GPP = 0.53. The incorporation of these ratios has been a very practical approach to represent autotrophic respiration in many ecosystem models, particularly if the research questions involved only concern net fluxes of carbon between ecosystems and the atmosphere.

Although a large proportion () of carbon may be respired on an annual basis from ecosystems as postulated by Waring, Landsberg, and Williams (1998), this carbon is not necessarily fixed from the same year or growing season. Photo-assimilates and structural tissue 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.

Models in which autotrophic respiration is computed as a constant proportion of GPP following Waring, Landsberg, and Williams (1998)’s approach are a special case of the GMRP, but excluding any maintenance respiration; i.e., respiration is only a function of growth. However, models that would follow the GMRP would compute respiration based on growth (possibly a function of GPP) and on the current biomass stock that needs to be maintained.

We are not aware of any land surface model that implements the GMWRP or the GP. On the contrary, many land surface models compute autotrophic respiration as a function of growth (GPP) as demonstrated by research on the matrix approach (Y. Luo et al. 2017).

The matrix representation of Y. Luo et al. (2017) synthesizes well the most common choice to represent respiration and carbon balances in ecosystem models, and can be written in matrix form as

where is a vector of ecosystem carbon pools, is a function of carbon inputs to the ecosystem, generally obtained as , where is autotrophic respiration. Then, NPP is allocated to ecosystem compartments such as foliage, stem, and roots according to the vector of allocation coefficients . The product of 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 transfers among compartments. For vegetation compartments, 100% of all outputs are transferred to litter and soil pools, because autotrophic respiration is already accounted for in the first term of equation [[eq:Luomodel]](#eq:Luomodel). This modeling choice implies that the carbon used for autotrophic respiration never enters a particular vegetation compartment and does not spend any time there. It also implies that the respiration paradigm only involves growth respiration and none of the other conceptual paradigms identified by Amthor (2000).

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 biometric data in tropical forests (Malhi, Doughty, and Galbraith 2011; Malhi et al. 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. Litton, Raich, and Ryan (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 is originally defined by Litton, Raich, and Ryan (2007).

## Representation of C allocation in models

A very common approached implemented in ecosystem models is to partition the *net* carbon gained through photosynthesis. This net gain is often calculated by subtracting from GPP. Most models distinguish two types of autotrophic respiration: growth respiration, and maintenance respiration. Growth respiration represents the cost of growing organs, which is often expressed as a percentage of the C influx (in most cases GPP) that cannot be used to build new tissues and is independent from the amount of C stored in the vegetation compartments. Maintenance respiration, in contrast, is the metabolic cost of maintaining the existing tissue, and it is usually computed as a proportion of the current carbon stock, but there is inconsistency on how this is actually implemented in many models.

We reviewed the mathematical structure of 18 ecosystem models, with particular attention to the functions implemented for carbon allocation. We found that half of the models (nine) calculate the net carbon gain by subtracting both growth and maintenance respiration from GPP. These models include ISAM (Masri et al. 2013), IBIS (Foley et al. 1996), CTEM (Arora and Boer 2005), HAVANA (Haverd et al. 2016), and JeDi-DGVM (Pavlick et al. 2013). In the model proposed by Trugman et al. (2018) growth respiration and respiration from root and stem depend on the C stocks, and the net C gain is partitioned to a non-structural C compartment (NSC), from which it is redistributed. In ACONITE (Thomas and Williams 2014), there is a maintenance respiration compartment that receives C from the labile and bud C compartments, not from the leaves, wood and roots. In the model proposed by Murty and McMurtrie (2000) there are different maintenance respiration variables, but only one depends on a C stock: the annual maintenance respiration rate of sapwood. Finally, in FOREST-BGC (Running and Coughlan 1988) the growth respiration and available C are calculated yearly, while the maintenance respiration is calculated daily from the C stocks.

The other nine models do not consider the stock-dependent maintenance respiration. Instead, some models explicitly claim that given the linear relationship between C canopy respiration and canopy photosynthes, the autotrophic respiration is a fixed fraction of the total photosynthetic fixation. Some models that fall into this category are CABLE (Wang, Law, and Pak 2010), G’DAY (Comins and McMurtrie 1993), DALEC (Williams et al. 2005), CASA (Potter et al. 1993), and TECO (Yiqi Luo, Weng, and Yang 2012). Other models, such as the one proposed by HILBERT and REYNOLDS (1991) calculate the net C gain by subtracting dark respiration from GPP. Finally, three of the 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 the model proposed by (DeAngelis et al. 2012) whose net carbon production depends on leaf C.

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. Only in a few models maintenance respiration is subtracted from a carbon stock such as a labile pool or other vegetation compartment.

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

The modeling choice of allocating carbon after autotrophic losses has an impact on the age of carbon respired from ecosystems. This age of carbon can be obtained indirectly from simulation models. Although most models do not represent carbon age explicitly, it can be computed using other computational approaches.

The age of respired carbon from ecosystem is characterized by its transit time distribution (Bolin and Rodhe 1973; Thompson and Randerson 1999; Carlos A. Sierra, Estupinan-Suarez, and Chanca 2021). 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 carbon to a model at equilibrium and observing the respiration flux over time. These distributions can also be obtained using the analytical formulas developed by Metzler and Sierra (2018) for models in equilibrium, or the approach described in Metzler, Müller, and Sierra (2018) for models out of equilibrium.

For illustration purposes, we will show here predictions from the global carbon model developed by Emanuel, Killough, and Olson (1981) and used by Thompson and Randerson (1999) to illustrate differences between GPP- and NPP-based allocation schemes.

At equilibrium, the GPP-based version of the model shows a continuous distribution of carbon that decreases with transit time (Figure [2](#fig:GPPversusNPP)). 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 zero, and respiration in later years is only contributed by the heterotrophic pools. The median age of the respired carbon (50% quantile of the transit time distribution) in the GPP-version of the model is 2.3 yr, i.e. 50 % of respired carbon is respired in less the 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.

![Transit time distributions obtained from the GPP- and the NPP-based versions of the model. 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. ](data:application/pdf;base64,)

Transit time distributions obtained from the GPP- and the NPP-based versions of the model. 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.

The GPP-based version of the model predicts a continuum of ages of respired carbon both for autotrophic and heterotrophic respiration (Figure [3](#fig:TTcontributions)). Although a large portion of autotrophic respiration is very young ( year), a significant proportion is older and can be respired years after photosynthetic fixation.

![Contribution of autotrophic and heterotrophic respiration to the transit time distribution in the GPP-based version of the model. The age distribution of total ecosystem respiration is equivalent to the transit time distribution of the ecosystem. ](data:application/pdf;base64,)

Contribution of autotrophic and heterotrophic respiration to the transit time distribution in the GPP-based version of the model. The age distribution of total ecosystem respiration is equivalent to the transit time distribution of the ecosystem.

# 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) (Mariah S. Carbone and Trumbore 2007; MARIAH S. Carbone et al. 2007; Mariah S. Carbone et al. 2013; Muhr et al. 2013, 2018; Trumbore et al. 2015). In vegetation compartments, studies have focused mostly on individual trees rather than on collection 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 (Mariah S. Carbone and Trumbore 2007), while in roots and stems the respired carbon is on average older than one year old, 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, Mariah S. Carbone et al. (2013) reported ages of the respired CO by the stem of *Acer rubrum* trees of 1.5 and 0 yr during spring and late summer, respectively. Muhr et al. (2013) reported ages of 2.5 and 3.3 yr for CO respired from the stem of *Simaruba amara* trees during the dry and the wet season, respectively; 2 years old CO from the stem of *Tachigali paniculata*; and 4.5 and 4 yr old CO 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 respired by in-stem samples of *Dacriodes microcarpa*, and 2.5 and 5 years old for CO from *Ocotea leucoxylon* during the dry and wet season, respectively. Some studies have also reported several years old respired CO, ranging from 1 to 5 yr from roots. Most of these studies report mean values of 4 years old respired carbon from roots (Czimczik et al. 2006; Schuur and Trumbore 2006; Mariah S. Carbone and Trumbore 2007), but younger CO (0.6 years old) has been also reported by Hilman et al. (2021).

Physical damage such as girdling increases the age of the respired CO. For example, Muhr et al. (2018) reported 1 year old CO respired by healthy *Scleronema micranthum* trees and 14 years old CO respired by trees after one year of girdling. Also, Hilman et al. (2021) reported increases in the age of the respired carbon from roots going from 0.6 years old from not girdled trees to 1.3 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 old, but older 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-Ramı́rez et al. 2020). This empirical evidence is consistent with models in which carbon allocation is based on GPP.

![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. Additional details are presented in Supplementary Table 1.](data:application/pdf;base64,)

Age of C in respired CO 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. Additional details are presented in Supplementary Table 1.

# 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 biosphere.

As radiocarbon measurements become increasingly available for plant parts and respired CO 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 in NPP-based models predicts an age of respired carbon as zero, inconsistent with radiocarbon measurements. Therefore, by construction, NPP-based allocation schemes cannot be used to constraint carbon allocation and respiration functions in models.

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 the underlying probability distribution that this mean transit time characterize. As we have seen here, the median transit time can deviate strongly from the mean, and the possibility to compute entire transit time distributions provide very useful information to integrate processes occurring at very different timescales (Carlos A. Sierra, Estupinan-Suarez, and Chanca 2021). 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 on the timescales of carbon exchange between ecosystems and the atmosphere.

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 from the terrestrial biosphere show a large difference between the GPP- and NPP-based versions of the simple model (Figure [5](#fig:radiocarbon)). Because carbon spends less time in NPP-based representations, 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).

![Radiocarbon in respired CO_2 predicted by the two versions of the model. ](data:application/pdf;base64,)

Radiocarbon in respired CO predicted by the two versions of the model.

# Summary and recommendations

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 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 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 maintain metabolic processes (Ogle and Pacala 2009; Herrera-Ramı́rez et al. 2020). Ultimately, the process of respiration in cells is based on the oxidation of organic molecules, which are part of the carbon inventory of an ecosystem.

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