Coarse woody debris are buffering mortality-induced carbon losses to the atmosphere in tropical forests

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1. Introduction

Across tropical forests, inventory plots provide key evidence of pervasive changes in forest biomass. The data from different networks of forest inventory plots have been used to estimate the mean carbon sink in tropical forest biomass, and its changes due to disturbances and other environmental drivers (Phillips et al. 2002, Gloor et al. 2009, Lewis et al. 2009, Pan et al. 2011, Mitchard 2018). For example, previous studies showed emerging relationships between biomass losses, gains, and cumulative water deficits during drought years in the Amazon (Phillips et al. 2009, Lewis et al. 2011) and a decreased trend of the carbon sink in biomass across the Amazon as a result of increased tree mortality (Brienen et al. 2015), whereas no detectable trend was found for Africa (Hubau et al. 2020).

In the above-mentioned and inventory-based studies (Brienen et al. 2015, Hubau et al. 2020), the carbon balance of forest aboveground biomass (AGB) is calculated as a difference between carbon gains (tree recruitment and growth) and losses (tree mortality and decomposition) across successive sampling campaigns. Such changes in forest aboveground biomass (ΔAGB) has been interpreted as being equivalent to the net land–atmosphere carbon exchange. We argue here that this interpretation is inaccurate because tree mortality does not cause an instantaneous CO₂ emission to the atmosphere, rather a lagged CO₂ emission from decaying coarse woody debris (ΔCWD), litter, and soil pools. Ignoring soil, branch, and fine litter changes, net biome productivity in biomass (NBₚ) accounts for the net change of live and dead biomass in terrestrial ecosystems at large temporal and spatial scales, and can be calculated as NBₚ = ΔAGB + ΔCWD.

In this study, we adopt a simple first-order kinetics model to simulate carbon emissions from the decomposition of CWD from dead trees at the scale of continental African and Amazonian wet tropical forests. This is achieved by using observations of stocks and turnover rates of the CWD carbon pool. Our objective is to provide insight into the difference between NBₚ and ΔAGB. To do so, we simulate the decay of CWD lagging tree mortality from a previous forest inventory synthesis. The key application is to contrast the reported saturation of the increase of ΔAGB (Hubau et al. 2020) with the trend of NBₚ. We hypothesize that NBₚ should saturate less rapidly than ΔAGB due to the fact that a large fraction of the carbon in dead trees converted to CWD has not yet been released to the atmosphere.

2. Modeling the lag in the mortality-related carbon release

Mortality of whole trees or branches forms CWD that can be decomposed by microbial processes in the soil. In this study, for the Amazonian forests, we use field-measured and estimated CWD decomposition rates from Palace et al. (2012) and Brienen et al. (2015) (see supplementary material which is available here stacks.iop.org/ERL/16/011006/mmedia). Assuming that influx and outflux are in approximate equilibrium, the decomposition rates values reported by Brienen et al. (2015) and Palace et al. (2012) were calculated using observed CWD production divided
by observed CWD stock (labeled as ‘Measured’ in figure 1). Besides, Palace et al (2012) also estimated the decomposition rates values at various sites without observed CWD production, using a simple estimate of CWD production, i.e. the product of biomass and a constant mortality rate of 0.02 yr$^{-1}$ (labeled ‘Estimated’ in figure 1). Here we use the same method to estimate decomposition rates using aggregated forest inventory data from Pan et al (2011). That is, we calculate CWD production using the mean forest total living biomass and a mortality rate of 0.02 yr$^{-1}$; and inferred the mean CWD decomposition rate as the ratio of production to their reported mean CWD stock.

For Amazonian forests, based on field measurements (Palace et al 2012, Brienen et al 2015), we find CWD decomposition rates ranging from 0.01 to 0.56 yr$^{-1}$, with a mean value of 0.20 yr$^{-1}$; This is equivalent to a turnover time of ~5 year. The large spread comes from inter-plot differences. Using mean inventory data around the years 1990, 2000 and 2007 (Pan et al 2011), we find CWD decom- position rates ranging from 0.10 to 0.11 yr$^{-1}$; This is equivalent to a turnover time of ~9 years. For African forests, no field data were available and the mean inventory data from Pan et al (2011) provide a mean value of 0.09 yr$^{-1}$ (turnover time ~11 years). The decomposition rates of CWD appear to be slightly lower in African forests compared to Amazon forests potentially resulting in longer carbon turnover times, although this difference needs to be confirmed by field measurements of CWD production and stock.

Through decomposition, carbon from CWD is partly released to the atmosphere via heterotrophic respiration, partly transformed to fine litter and soil carbon pools via fragmenting litter, and partly leached to dissolved organic carbon. Respiration comprises the majority of carbon lost during CWD decay (Harmon et al 2020), so we assumed here that the decay loss of CWD goes directly into the atmosphere as CO$_2$. The change in carbon stocks of CWD over time on a yearly time step $d$CWD$/dt$ is calculated by the difference between incoming and outgoing fluxes, given by:

$$d\text{CWD}/dt = I(t) - k \text{CWD}(t). \tag{1}$$

The incoming flux, $I(t)$ is the mortality of trees and other components (e.g. branches) forms at time $t$. Here we make the approximation that $I(t)$ can be estimated from above- and below-ground tree biomass mortality, thus ignoring branches and woody debris intercepted by the canopy. AGB in living stems from inventory plots is calculated by using an allometric equation with tree diameter, tree height and wood mass density (Chave et al 2014). Below-ground tree biomass mortality is estimated using regionally specific root–shoot ratios from FRA 2020 report (i.e. Africa: 0.30; Amazon: 0.24; FAO 2020). We acknowledge that this approach can underestimate the total CWD inputs, by not considering the branches and other woody debris. The outgoing flux is assumed to follow the first-order decay equation (1) with a constant decomposition rate $k$ deduced by the different methods as explained above. The non-decomposed CWD fraction during year $t$, i.e. $(1 - k) \times \text{CWD}(t)$, remains in the CWD pool to be decomposed in subsequent years.

Dead trees decay slowly (Palace et al 2012) and thus delay CO$_2$ emissions to the atmosphere after big mortality events. As shown in figures 2(a) and (b), when we apply equation (1) to AGB data from long-term monitoring plots (Hubau et al 2020), the net CO$_2$ losses including CWD buffering in both Amazonian and African forests during the 1980s are smaller than when assuming yearly $I(t)$ is returned immediately as CO$_2$ to the atmosphere, for instance as
The buffering effectson carbon balance and its decadal trends

The gross carbon losses from AGB of intact tropical forests are shown in figures 2(a) and (b), using data from Hubau et al. (2020). These gross carbon losses from biomass are not gross CO$_2$ emissions to the atmosphere, since carbon from dead wood is transformed to CWD before it gets oxidized into CO$_2$. Considering the decay rate of CWD fed by tree mortality (see details in section 2), we find that the interannual variability in the gross carbon loss flux to the atmosphere is greatly reduced due to carbon remaining in CWD after mortality, in both Amazon and African forests (figures 2(a) and (b)). The reconstructed NBP$_B$ including the mass balance of CWD is shown in figures 2(c) and (d). It shows a dampening of quasi-annual NBP$_B$ fluctuations compared to those of ∆AGB. In figure 2(e), comparing decadal trends of NBP$_B$ versus ∆AGB, we observe a faster and significant decrease of the NBP$_B$ carbon sink in the Amazon during 1981–2000 but a slower decrease during 2001–2012. A smaller decadal trend of NBP$_B$ versus ∆AGB typically occurs if the decomposition rate $k$ is greater than 0.1 (figure 3(a)). For Africa, we find no trend of NBP$_B$ compared to the positive trend of ∆AGB reported by Hubau et al. (2020) during 1981–2000, and a slight, significant and negative trend of NBP$_B$ after 2001, regardless of decomposition rates $k$ (figure 3(b)). Compared to ∆AGB trends, our estimates of NBP$_B$ trends give a more nuanced picture of the ‘divergence’ of carbon sinks highlighted by Hubau et al. (2020). Namely,
the African and Amazonia sinks from AGB diverge since the early 1990s, whereas the NBP生命周期 sinks diverge only after the late 1990s. Accounting for the buffering effect of CWD, regional NBP生命周期 estimates are expected to be more directly comparable to net land–atmosphere CO2 exchange estimates independently obtained by atmospheric inversions. Nonetheless, the definition of net CO2 fluxes estimated by atmospheric inversions is different from regional NBP生命周期 in our study. The component fluxes of soil and litter decomposition, leaching from soil and subsequent river outgassing (Lauerwald et al 2015, Hastie et al 2018) are included in inversions, but not in our definition of NBP生命周期. The role of soil and litter respiration coupled to AGB and CWD dynamics is not modeled in this study, due to the lack of long-term respiration data across sites. Specific site studies showed that the fraction of CWD entering into soil organic carbon (SOC) pools and being respired has a significant effect on the net land–atmosphere CO2 flux at the ecosystem scale (Chambers et al 2004, Sierra et al 2007). With litter and SOC turnover rates from tropical sites, our approach could be extended to include subsequent carbon loss pathways due to respiration as a result of tree mortality.

The effects of including CWD on NBP生命周期 trends and inter-annual variability depend on the values of CWD decomposition rates: a high decomposition rate induces less buffering of carbon emissions from CWD. The value of k is determined by tree species, diameter, position (i.e. standing versus downed), canopy openness, as well as microclimate (Harmon et al 2020). However, due to a lack of relevant observations, we coarsely simplify the analysis and use regionally averaged constant decomposition rates for Amazonian and African forests. In addition, disturbance events such as fire, extreme drought, insect outbreaks, storms, and land management can also alter decomposition rates, influencing the terrestrial carbon dynamics (Luo et al 2017, Pugh et al 2019), but the box model of equation (1) does not explicitly incorporate the impact of disturbances on decay rates.

These points suggest that higher decomposition rates could be associated with forests with higher mortality rates, which tend to have large size, low wood density, and experience higher disturbance rates (Phillips et al 2010), resulting in covariance between CWD decay and aboveground turnover that is not accounted for in this study. Future work is needed to quantify the effects of CWD decomposition on trends and inter-annual variability in carbon sink for different tree sizes, species, traits, disturbance history, and not just for tropical forests, but for semi-arid, temperate and boreal ecosystems. This buffering capacity of CWD may have even longer legacy effects when the value of the decomposition rate is even smaller resulting in longer carbon turnover times in semi-arid and cooler temperate forests.

In summary, our analysis helps carbon cycle scientists and policy-makers to appreciate that results from Hubau et al (2020) and similar studies do not represent carbon fluxes exchanged with the atmosphere contributing to annual variations of the CO2 growth rate. We propose a simple attempt to translate AGB carbon changes observed on the ground into the CO2 flux to the atmosphere. We estimate the lagged CO2 release via CWD decomposition after tree mortality in Amazonian and African forests. When considering CO2 released by CWD decay, net CO2 losses to the atmosphere in both Amazonian and African forests during the 1980s are smaller than observed biomass drops. The high tree mortality during the 1980s legates a continuous CO2 loss in subsequent decades. Such persistent carbon losses after mortality can alter the trends of atmospheric CO2: more pronounced decreases of the NBP生命周期 carbon sink in the Amazon during 1981–2000 but a weaker increase of carbon sink in Africa during the past three decades, once the lagged CWD decay are accounted for. Local evidence that CWD emissions partly or entirely offset biomass gains (recovery) has also been documented at old-growth Amazonian forest sites. For instance, Rice et al (2004) found that losses from CWD turned their study site into a source, whereas
tree gains were a sink. A consistent result was reported by Saleska et al (2003) at the Santarem forest sites recovering from disturbance that occurred 30 years ago. These site-level results show a net AGB gain but a new CO2 source, supporting our perspective that the incomplete characteristics of carbon balance could lead to a biased estimate of carbon flux in the tropics. This highlights the importance of understanding how tree mortality and subsequent decomposition affect the carbon balance of tropical ecosystems. The missing component fluxes, such as soil and litter respiration should be taken into account in the future, further improving our predictions of regional carbon dynamics under future climate scenarios.

Data availability statement

The inventory data from Hubau et al (2020) are openly available at the following URL/DOI: https://doi.org/10.1038/s41586-020-2035-0. The plot-scale CWD decomposition rate k estimates from Amazonian forests from Brienen et al (2015) and Palace et al (2012) were listed in the supporting information.

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