



Explaining the seasonal cycle of the globally averaged CO₂ with a carbon-cycle model

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Abstract. The seasonal changes in the globally averaged atmospheric carbon-dioxide concentrations reflect an important aspect of the global carbon cycle: the gas exchange between the atmosphere and terrestrial biosphere. The data on the globally averaged atmospheric carbon-dioxide concentrations, which are reported by Earth System Research Laboratory of the US National Oceanic & Atmospheric Administration (NOAA/ESRL), could be used to demonstrate the adequacy of the global carbon-cycle models. However, it was recently found that the observed amplitude of seasonal variations in the atmospheric carbon-dioxide concentrations is higher than simulated. In this paper, the factors that affect the amplitude of seasonal variations are explored using a carbon-cycle model of reduced complexity. The model runs show that the low amplitude of the simulated seasonal variations may result from underestimated effect of substrate limitation on the seasonal pattern of heterotrophic respiration and from an underestimated magnitude of the annual gross primary production (GPP) in the terrestrial ecosystems located to the north of 25° N.

1 Introduction

The global mean monthly atmospheric concentrations of carbon dioxide provided by NOAA/ESRL (Conway and Tans, 2012) show that the carbon storage of the atmosphere undergoes regular seasonal changes. The amplitude of seasonal variations in the atmospheric carbon storage puts certain constraints on the choice of parameters in the models of the global carbon cycle and the joint carbon-climate models. It would be natural to expect that models are tuned to reproduce the CO₂ growth curve – the basic scientific evidence of global change – but this not the case. One may find papers demonstrating that carbon-cycle models coupled with atmospheric transport models could reproduce seasonal cycles of CO₂ concentrations at some locations (Heimann et al., 1998; Dargaville et al., 2002; Randerson et al., 2009; Cadule et al., 2010; Anav et al., 2013). However, it is difficult to find an article comparing simulated seasonal variations in the atmospheric carbon storage with the globally averaged monthly concentrations of carbon dioxide. A recent article (Chen, 2011) reporting the results of such comparison

brings bad news: the observed amplitude of seasonal variations in the atmospheric carbon storage is larger than simulated. Where does this discrepancy come from? According to Chen (2011), it comes from the “representation error” of observation stations: “The apparent discrepancy between modeling results and observations results from the ‘representation error’ of observation stations” (Chen, 2011). This assumption is challenged here by demonstrating that the discrepancy can be reconciled through model tuning.

2 Methods

2.1 Net carbon exchange between the atmosphere and other pools

2.1.1 Observations

The seasonal cycle of the atmospheric carbon storage reflects the seasonal cycle of the net carbon exchange between the atmosphere and other pools. The detrended net exchange (N_a) could be derived from the detrended atmospheric

carbon storage (dC_a), which, in turn, could be estimated from the detrended globally averaged monthly concentrations of carbon dioxide at sea surface ($d[CO_2]$) reported by NOAA/ESRL (Conway and Tans, 2012), assuming that $dC_a(m) = 2.13 \times d[CO_2](m)$. Since $dC_a(m)$ is the value of dC_a in the middle of the month m , the value of dC_a at the beginning of the month m is calculated as the mean of its values in the middle of this month and in the middle of the preceding month; that is, as $(dC_a(m-1) + dC_a(m))/2$, and the value of dC_a at the end of the month m should be calculated as the mean of its values in the middle of this month and in the middle of the following month. That is, as $(dC_a(m) + dC_a(m+1))/2$. Then $N_a(m)$ should be calculated as the difference between the value of dC_a at the end of the month m and its value in the beginning of the month m :

$$N_a(m) = \frac{dC_a(m) + dC_a(m+1)}{2} - \frac{dC_a(m-1) + dC_a(m)}{2}, \quad (1)$$

which gives

$$N_a(m) = \frac{dC_a(m+1) - dC_a(m-1)}{2}. \quad (2)$$

The accuracy of monthly N_a estimates is determined by the accuracy of monthly $d[CO_2]$ estimates. Since monthly $d[CO_2]$ estimates are derived from local observations (Masarie and Tans, 1995), the accuracy of monthly N_a estimates depends on the adequacy of the observation network. Besides, the “characteristic vertical mixing time of the troposphere is little more than month” (Bolin, 1976), and hence it is not clear if the monthly globally averaged concentration at sea surface provides a good approximation to the monthly globally averaged concentration in the whole volume of the earth’s atmosphere.

Another method for estimating N_a (so-called inversion of simulated tracer transport) is not based on the assumption that the atmosphere is well mixed vertically: mixing processes are described using an atmospheric transport model. This method is theoretically more sound, but fairly complicated. The estimates of N_a obtained using this method and various atmospheric transport models in the course of the TransCom 3 experiment (Gurney and Denning, 2013) are presented in Fig. 1 in the form of a box-and-whisker diagram. A total of 12 atmospheric transport models were used in this experiment to assess sensitivity of the flux estimates to the choice of transport model (Gurney et al., 2004). Besides, a Carnegie–Ames–Stanford Approach (CASA) model of net ecosystem production (Randerson et al., 1997) was used to keep the estimated fluxes within biogeochemically realistic bounds. Thus obtained estimates, $N_{a,v}$, are not radically different from the estimates inferred from globally averaged concentrations at sea surface, $N_{a,s}$, but they have a great advantage: one may easily form an impression about the $N_{a,v}$ accuracy from the box-and-whisker diagram.

In principle, N_a could also be derived from observations at Fluxnet sites (Falge et al., 2005). Although these observations are used mainly for evaluating the ability of global

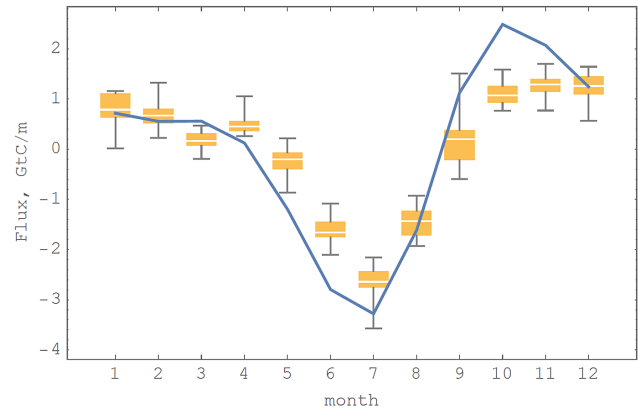


Figure 1. The seasonal cycle of the detrended net carbon exchange between the atmosphere and other pools derived from globally averaged monthly surface CO₂ concentrations in 1995–2005 (blue) as compared to the detrended TransCom 3 seasonal CO₂ flux (orange) estimated from atmospheric inversions (Gurney and Denning, 2013).

scale models to reproduce land–atmosphere fluxes at local scale, the large size of the Fluxnet network makes it reasonable to use Fluxnet observations for estimating N_a : this could be done by applying Masarie–Tans algorithm (Masarie and Tans, 1995) or more complicated interpolation methods (Jung et al., 2011). Global upscaling of local land–atmosphere fluxes is a fairly new direction of research that, in the near future, may deliver the data sets that are needed for estimating N_a .

2.1.2 Modeling

The monthly N_a estimates could be also calculated using the following equation:

$$N_a(m) = -GPP(m) + R_a(m) + R_h(m) + v_a(m), \quad (3)$$

where GPP, R_a , and R_h are gross primary production, autotrophic respiration, and heterotrophic respiration of the terrestrial ecosystems, and v_a is net carbon exchange between the atmosphere and remaining carbon pools.

The seasonal cycle of GPP, R_a , and R_h is simulated here using the concepts of the MONTHLYC model (Box, 1988) and the global fields of monthly actual evapotranspiration (Willmott, 1985) and monthly air temperature (Leemans and Cramer, 1991) gridded at a $0.5^\circ \times 0.5^\circ$ resolution.

The seasonal cycle of GPP is determined in the MONTHLYC model by the monthly actual evapotranspiration, AET(m):

$$GPP(m) = \frac{AET(m)}{\sum_{m=1}^{12} AET(m)} GPP_{ann}, \quad (4)$$

where GPP_{ann} (the annual GPP) is derived from the Montreal NPP model.

The Montreal net primary production (NPP) model relates annual net primary production (NPP_{ann}, in gC m⁻² yr⁻¹) to annual actual evapotranspiration (AET_{ann}, in mm yr⁻¹) (Box, 1988):

$$\text{NPP}_{\text{ann}} = 1350 \cdot \left(1 - e^{-0.0009695 \cdot (\text{AET}_{\text{ann}} - 20)}\right), \quad (5)$$

and GPP_{ann} is derived from NPP_{ann} using the empirical equation (Box, 1988):

$$\text{GPP}_{\text{ann}} = -1863 \cdot \ln(1 - \text{NPP}_{\text{ann}}/1350), \quad (6)$$

which gives

$$\text{GPP}_{\text{ann}} = 1.8062 \cdot (\text{AET}_{\text{ann}} - 20), \quad (7)$$

where 1.8062 is the value characterizing the water-use efficiency (WUE) – the amount of GPP in gC produced per 1 L of the water transpired. Hence, the general form of this equation is as follows:

$$\text{GPP}_{\text{ann}} = \text{WUE} \cdot (\text{AET}_{\text{ann}} - 20). \quad (8)$$

The monthly values of R_a in the MONTHLYC model are proportional to $Q_{10}^{\frac{T(m)-10}{10}}$ ($Q_{10} = 2$)

$$R_a(m) = \frac{Q_{10}^{\frac{T(m)-10}{10}}}{\sum_{m=1}^{12} Q_{10}^{\frac{T(m)-10}{10}}} R_{a,\text{ann}}, \quad (9)$$

where $T(m)$ is monthly air temperature and $R_{a,\text{ann}}$ is the annual autotrophic respiration calculated as the difference between GPP_{ann} and NPP_{ann}:

$$R_{a,\text{ann}} = \text{GPP}_{\text{ann}} - \text{NPP}_{\text{ann}}. \quad (10)$$

The monthly values of heterotrophic respiration from each litter pool depend in the MONTHLYC model on the rates of litter decay and the storage of litter:

$$R_{h,i}(m) = r_i(m) s_i(m), \quad (11)$$

where the monthly values of decay rates are proportional to monthly values of AET:

$$r_i(m) = \frac{\text{AET}(m)}{\sum_{m=1}^{12} \text{AET}(m)} r_{a,i}, \quad (12)$$

and $r_{a,i}$ depends on the annual amount of AET (Box, 1988) as follows:

$$r_{a,i} = r_{0a,i} \times 10^{-1.4553 + 0.0014175 \cdot \text{AET}_{\text{ann}}}. \quad (13)$$

The monthly values of litter storages satisfy the following difference equations in the MONTHLYC model:

$$s_i(m+1) = s_i(m) + p_i(m) - R_{h,i}(m), \quad (14)$$

where $p_i(m)$ is the input of organic matter to the i th pool of litter. They are found by iterations.

Up until now, all of the modeling formulation directly follows Box (1988). Modifications that I introduced to the MONTHLYC model were as follows.

I use two pools: the pool of slowly decaying fractions and the pool of quickly decaying fractions, whereas Box (1988) used three litter pools: above-ground true litter (mostly leaves), root litter, and large woody debris (deadfall). The annual heterotrophic respiration is thus divided into heterotrophic respiration related to slowly decaying fractions of litter ($R_{h,s}$) and that related to quickly decaying fractions ($R_{h,q}$). The adequacy of this approach is discussed in the Appendix A1.

The seasonal changes in the storage of slowly decaying litter are small in comparison to its average value, and so the seasonal cycle of $R_{h,s}$ reflects that of the rate of decay, which is assumed to be proportional to AET(m):

$$R_{h,s}(m) = \frac{\text{AET}(m)}{\sum_{m=1}^{12} \text{AET}(m)} R_{h,s,\text{ann}} \quad (15)$$

and

$$R_{h,s,\text{ann}} = (1 - \phi) \text{NPP}_{\text{ann}}, \quad (16)$$

where ϕ is the share of quickly decaying fractions in the litterfall, and $R_{h,s,\text{ann}}$ is the part of heterotrophic respiration related to slowly decaying fractions of litter, which, in the case of the detrended carbon cycle, is equal to the corresponding part of NPP_{ann}.

The storage of quickly decaying fractions is sensitive to the seasonal pattern of litterfall. Since deciduous trees shed leaves at the end of growing season, the part of heterotrophic respiration, which is related to quickly decaying fractions, may depend on the substrate availability. The seasonal changes in the storage of quickly decaying fractions of litter (s) are modeled here by the ordinary differential equation:

$$\frac{ds}{dt} = -r(t)s, \quad (17)$$

where $r(t)$ is the rate of litter decay, and t is the time elapsed since the end of growing season. The function $r(t)$ is a periodical continuous function, $r(t+12) = r(t)$, the average value of which during the month m is proportional to monthly values of AET:

$$\int_{m-1}^m r(t) dt = \frac{\text{AET}(m)}{\sum_{m=1}^{12} \text{AET}(m)} \int_0^{12} r(t) dt. \quad (18)$$

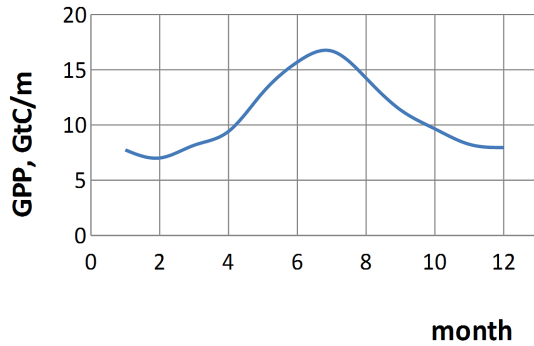


Figure 2. Seasonal cycle of the gross primary production (GPP), as calculated using Eqs. (4)–(7).

If litterfall occurs only at the end of growing season, then $s(0) = s(12) + p$, where p is equal to $\phi \cdot \text{NPP}_{\text{ann}}$. In this case,

$$s(n) = \frac{\phi \cdot \text{NPP}_{\text{ann}}}{1 - e^{-\int_0^n r(t) dt}} e^{-\int_0^n r(t) dt}, \quad (19)$$

where n is the number of months elapsed since the end of growing season.

The growing season ends at different times in different places, and hence, to calculate s in a given month m at a given location, one should know in which month, m_0 , the growing season ends at this location. If $m \geq m_0$, then $n = m - m_0$, and the storage of quickly decaying litter in a given month m is calculated using the equation

$$s(m, m_0) = \frac{\phi \cdot \text{NPP}_{\text{ann}}}{1 - e^{-\int_{m_0}^m r(t) dt}} e^{-\int_{m_0}^m r(t) dt}. \quad (20)$$

If $m < m_0$, then $n = 12 + m - m_0$, and $s(m, m_0)$ is calculated as follows:

$$s(m; m_0) = \frac{\phi \cdot \text{NPP}_{\text{ann}}}{1 - e^{-\int_{m_0}^{m+12} r(t) dt}} e^{-\int_{m_0}^{m+12} r(t) dt}. \quad (21)$$

Consequently, heterotrophic respiration related to decomposition of quickly decaying litter is calculated using the following equations:

$$R_{h,q}(m) = s(m-1; m_0) - s(m; m_0), \quad (22)$$

where the geographic distribution of m_0 is derived from the assumption that the growing season in the deciduous forests of the Northern Hemisphere normally ends when monthly air temperature drops below 10 °C (that is, in September or October), and that, in some other ecoregions, the end of growing

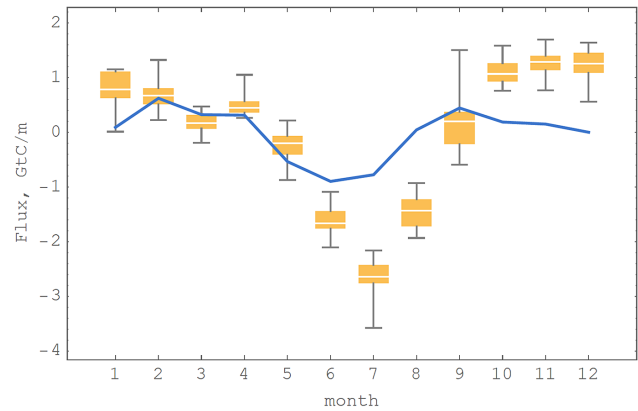


Figure 3. The seasonal cycle of $N_{a,\text{mod}}$ (blue) for $\text{WUE} = 1.8 \text{ gCL}^{-1}$, $Q_{10} = 2.0$, and $\phi = 0$, as compared to the detrended TransCom 3 seasonal CO₂ flux (orange) estimated from atmospheric inversions (Gurney and Denning, 2013).

season may occur due to the lack of precipitation, e.g., when monthly AET drops below 20 mm month⁻¹.

GPP, R_a , and R_h are the major drivers of the seasonal changes in the atmospheric carbon storage. The amplitude of seasonal changes in the carbon exchange between the atmosphere and the ocean is relatively small (e.g., Chen, 2011). The same can be said about the seasonal changes in the emissions from fossil fuels burning. Hence, one could assume that $N_{a,\text{mod}}(m) = -\text{GPP}(m) + R_a(m) + R_{h,s}(m) + R_{h,q}(m)$ may give a good approximation of $N_a(m)$ under some choice of ϕ , WUE, and Q_{10} values. This assumption was tested by numerical experiments. The results are discussed below.

3 Results and discussion

The global monthly GPP, calculated using Eqs. (4)–(7), has a peak when both $N_{a,v}$ and $N_{a,s}$ have a dip (Figs. 1–2), supporting the view that seasonal cycle of the globally averaged atmospheric CO₂ concentration at sea surface reflects the seasonality of plant activity (Keeling et al., 1996). The effect of GPP is reduced, however, by autotrophic respiration (R_a) that has a peak in the same month as GPP. The part of the heterotrophic respiration that results from the decay of slowly decaying fractions of litter ($R_{h,s}$) also has a peak at the same month as GPP. Consequently, the amplitude of the seasonal changes in $N_{a,\text{mod}}$ could be very narrow if compared to that of $N_{a,v}$ (Fig. 3).

The discrepancy between the amplitude of the seasonal changes in $N_{a,\text{mod}}$ and that of $N_{a,v}$ can be reconciled by increasing WUE, decreasing Q_{10} , and increasing ϕ . The “true” values of these model coefficients are not known, but they should fall within empirically established, or widely accepted, bounds. Jasechko et al. (2013) estimated the global WUE of the terrestrial biosphere to be $3.2 \pm 0.9 \text{ mmol CO}_2 \text{ per mol H}_2\text{O}$, which corresponds to the range from 1.5 to

2.7 gC per liter of water and suggests that 2.7 gC per liter of water can be taken as the highest possible estimate of WUE. Zhao and Running (2011) used 1.4 as the lowest possible estimate of Q_{10} . The highest possible estimate of ϕ cannot exceed the share of herbaceous fractions in the litterfall, which varies from 0.3 in forests to 0.9 in grasslands (Esser, 1984). Parton et al. (1987) divided herbaceous litter into the pool of structural C, the residence time of which is 3 years, and the pool of metabolic C, the residence time of which is 0.5 years. Hence, the highest possible estimate of ϕ cannot exceed the share of herbaceous fractions in the litterfall multiplied by the share of metabolic C compounds in the herbaceous litter. The latter depends on lignin/nitrogen ratio, and thus could be very small in evergreen needleleaf forests. Moreover, Parton et al. (1987) assumed that only 55 % of carbon is released to the atmosphere in course of fresh litter decomposition, whereas 45 % go to the pools of soil organic matter. Thus, the possible values of ϕ could range from 0.1 to 0.3, depending on the share of land covered by grasslands and broadleaf forests. Numerical experiments show that the amplitude of the seasonal changes in $N_{a,mod}$ can be roughly the same as the amplitude of the seasonal changes in $N_{a,v}$ under some values of WUE, Q_{10} , and ϕ that fall within the bounds mentioned above (Fig. 4).

This result demonstrates that amplitude of the seasonal cycle of the globally averaged monthly surface concentrations of carbon dioxide reported by NOAA/ESRL could be simulated with a carbon-cycle model. The simplicity of the model that is used in this study may raise doubts on its validity. Although the doubts of this sort are difficult to dispel due to the lack of standardized tools needed for adequate model evaluation (Alexandrov et al., 2011), the usage of the model could be legitimated as follows.

The purpose of the study is to understand the behavior of more complex models. Model complexity poses an obstacle for diagnosing the sources of discrepancy between model predictions and observations. Xia et al. (2013) show that one can overcome this obstacle by decomposing a complex model into traceable components. Another approach is to use minimal models; that is, to use the models of reduced complexity, which are designed to explain only certain aspects of a system (Evans et al., 2013). Many aspects of complex model behavior are beyond the scope of this study. Among them are the increasing amplitude of the seasonal changes in the globally averaged monthly concentrations of carbon dioxide (Graven et al., 2013) and the spatial distribution of soil carbon (Todd-Brown et al., 2013). The version of the MONTHLYC model is used as a minimal model; that is, it is used merely to explore the factors that affect the amplitude of seasonal changes in N_a .

One of these factors is substrate limitation, which may be caused by the shift between the phase of NPP seasonal cycle and the seasonal cycle of litterfall production. The models and submodels of litterfall production (e.g., Randerson et al., 1996; Potter et al., 1993; Box, 1988; Esser, 1987; Ito and

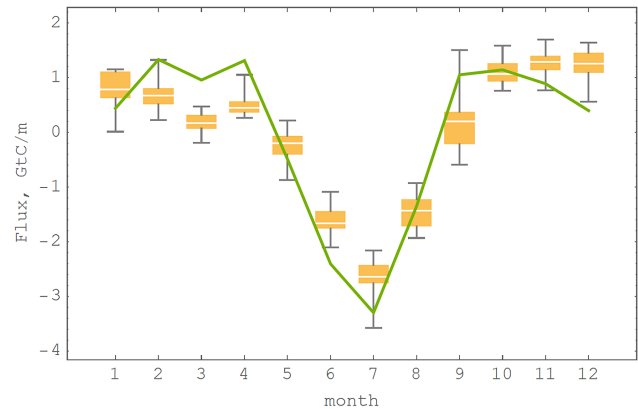


Figure 4. The seasonal cycle of $N_{a,mod}$ (green) for WUE = 2.7 gCL⁻¹, $Q_{10} = 1.4$, and $\phi = 0.2$, as compared to the detrended TransCom 3 seasonal CO₂ flux (orange) estimated from atmospheric inversions (Gurney and Denning, 2013).

Oikawa, 2002; Eliseev, 2011) often deal with such components as coarse woody debris, fine woody debris, leaf debris, and so on. In this study, all litter components were aggregated in two pools: slowly decaying fractions and quickly decaying fractions. The conceptual validity of this approach is explained in the Appendix A1. The pool of quickly decaying fractions is assumed to be refilled once per year (Fig. 5) and depleted in summer. During the period of the pool depletion, heterotrophs decomposing quickly decaying fractions become substrate-limited. This causes a decrease in monthly heterotrophic respiration below that expected from a model that does not take into account the effects of substrate availability. The decrease, which is referred to as substrate limitation (Randerson et al., 1996), depends on the share of quickly decaying fractions in the litterfall. Hence, the share of quickly decaying fractions in the litterfall is one of the parameters of the complex models of carbon cycle that are responsible for the amplitude of the simulated seasonal changes in N_a .

Another important factor is the annual magnitude of the terrestrial GPP. Beer et al. (2010) estimated it at $123 \pm 8 \text{ GtC yr}^{-1}$. This estimate is close to the estimate that can be obtained with the MONTHLYC model for the original setting of WUE: Eq. (7) gives 129 GtC yr^{-1} . If WUE is set at 2.7 gCL, Eq. (8) gives 193 GtC/year . The highest possible estimate of the terrestrial GPP could be assessed using the Osnabruck collection of data on NPP (Esser et al., 2000). The analysis of these data implies (Alexandrov et al., 1999) that the 90 % confidence interval for the estimate of the terrestrial NPP is 52–81 GtC yr^{-1} . Given that GPP is often estimated by doubling NPP, one may conclude that the highest possible estimate of the terrestrial GPP should not exceed 160 GtC yr^{-1} . The annual magnitude of the terrestrial GPP, perhaps, need not be set at 193 GtC yr^{-1} in more complex

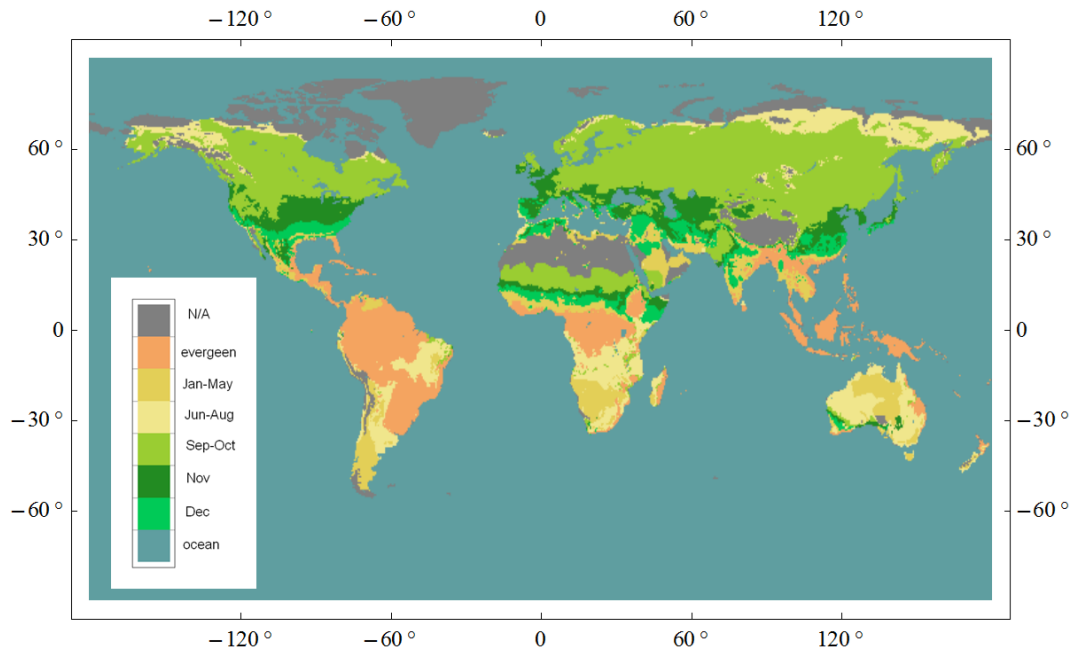


Figure 5. The month at which deciduous trees supposedly shed leaves due to the end of growing season.

models in which WUE may vary depending on the vegetation type and the phase of the growing season.

The data on seasonal changes in NEE (net ecosystem exchange) observed on Fluxnet sites (Falge et al., 2005) allows us to see whether the model applied at the global scale can reproduce the seasonal cycle of local NEE. The results of simulations for the “Hesse Forest” site (JHE99_dc_u0_mm.flx), presented in Fig. 6, show that the model can reproduce a large part of the amplitude of the NEE seasonal cycle if the model coefficients are set at the values that are used to reproduce the seasonal cycle of the globally averaged CO₂. At the same time, Fig. 6 shows that setting WUE at a constant value over the whole year may underestimate GPP at the beginning of the growing season.

The results of the TransCom 3 experiment (Gurney et al., 2004) allow us to evaluate the ability of the model to reproduce the seasonal cycle of regional carbon fluxes. As can be seen in Fig. 7, setting WUE (and other model coefficients) at globally uniform value puts limitations on the domain of model application.

For northern regions (Europe, boreal North America, and boreal Asia), the “green” version of the model (i.e., the version in which $WUE = 2.7 \text{ gCL}^{-1}$, $Q_{10} = 1.4$, and $\phi = 0.2$) fits the results of the TransCom 3 experiment better than the “blue” version of the model does (i.e., the version in which $WUE = 1.8 \text{ gCL}^{-1}$, $Q_{10} = 2.0$, and $\phi = 0$). However, for South and North Africa, the “blue” version outperforms the “green” version. It also outperforms the “green” version for South America. As for tropical Asia, both the green curve and blue curve fall within the wide range of uncertainty in TransCom’s estimates, which is explained as follows:

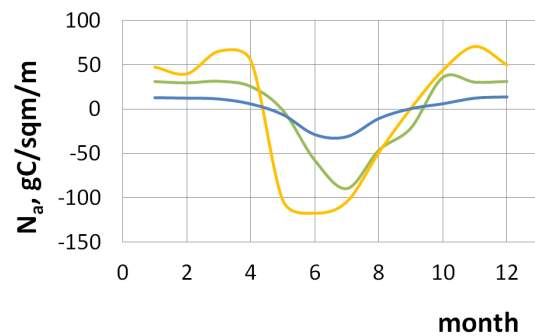


Figure 6. The seasonal cycle of the local $N_{a,mod}$ for $WUE = 2.7 \text{ gCL}^{-1}$, $Q_{10} = 1.4$, and $\phi = 0.2$ (green) as compared that for $WUE = 1.8 \text{ gCL}^{-1}$, $Q_{10} = 2.0$, and $\phi = 0$ (blue) and to the detrended NEE observed at the “Hesse Forest” site of Fluxnet (orange).

“Owing to limited CO₂ observations, tropical regions, particularly over land, show considerable uncertainty and may contain unrealistic seasonal swings in flux due to unconstrained adjustments to maintain the global mass balance constraint” (Gurney et al., 2004).

The model coefficients should be set on a regional basis to reproduce the seasonal cycle of regional carbon fluxes. This is a conclusion that can be drawn from Fig. 7. However, it would be wrong to assume that setting model coefficients on a regional basis would lead to dramatic changes in $N_{a,mod}$. The amplitude of seasonal changes in the total flux from Africa, South America, tropical America, tropical Asia, and Australia is much smaller than that of the total flux from

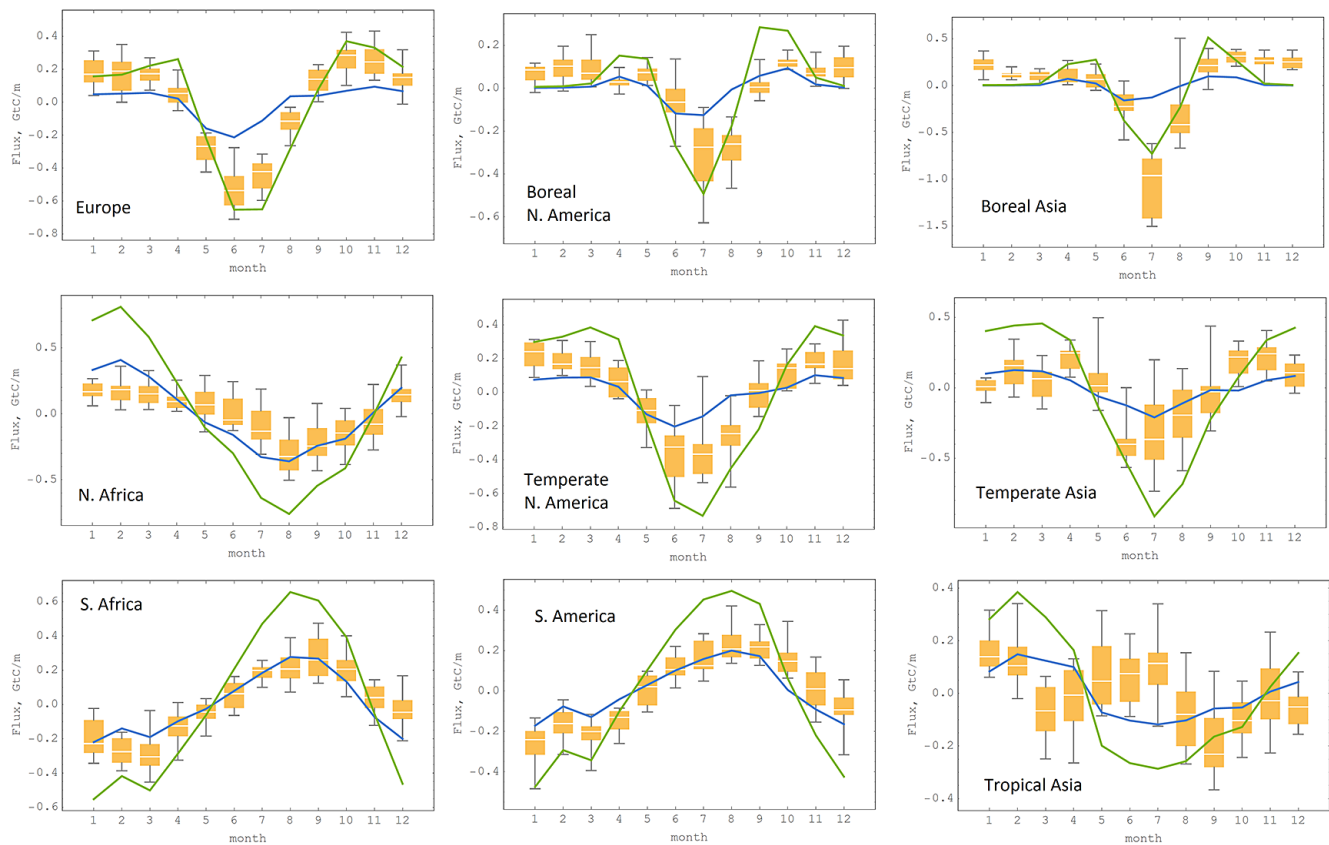


Figure 7. The seasonal cycle of the regional $N_{a,mod}$ for $WUE = 2.7 \text{ gCL}^{-1}$, $Q_{10} = 1.4$, and $\phi = 0.2$ (green) as compared to that for $WUE = 1.8 \text{ gCL}^{-1}$, $Q_{10} = 2.0$, and $\phi = 0$ (blue), and to the detrended TransCom 3 seasonal CO₂ flux (orange) estimated from atmospheric inversions (Gurney and Denning, 2013).

Europe, non-tropical North America, and non-tropical Asia. There is no need to raise WUE of the tropical and Southern Hemisphere ecosystems. It can be kept at 1.8 gCL^{-1} . Since most seasonal changes in $N_{a,v}$ can be attributed to seasonal changes in NEE in the ecosystems located to the north of 25N, the amplitude of $N_{a,mod}$ can be increased by raising WUE of these ecosystems.

The hypothesis that productivity of these ecosystems is currently underestimated and the hypothesis about the importance of substrate limitation are not mutually independent. The recent studies on microbial priming of soil organic matter decomposition (Heimann and Reichstein, 2008; Luo et al., 2011; Qiao et al., 2014) reveal the link between productivity and substrate limitation: increase in quickly decaying litterfall accelerates decomposition of “old” soil carbon.

Microbial priming of soil organic matter decomposition is one of the important mechanisms and processes that have not received proper attention in this study due to limitations of the MONTHLYC model. Hopefully, they will be addressed in further studies in which more detailed models will be used to test working hypotheses proposed in this paper.

4 Conclusions

The amplitude of seasonal changes in the globally averaged atmospheric CO₂ concentrations at sea surface characterizes an important aspect of the global carbon cycle. The fact that a complex carbon-cycle model cannot reproduce it (Chen, 2011) raises the question about the adequacy of this and other models. Complexity makes it difficult to trace a model inadequacy back to its source. Therefore, the model that is used in this study omits many important details for the sake of conceptual clarity. This allows us to reveal potential shortcomings. The low amplitude may result from underestimated annual magnitude of GPP in the terrestrial ecosystems located to the north of 25N and from underestimated effect of substrate limitation. The effect of substrate limitation could be lost if model structure does not include the pool of litterfall fractions, which are fully decomposed within a year. Such deficiency can be corrected through modeling the seasonal pattern of the herbaceous litterfall and estimating the share of quickly decaying fractions in the herbaceous litterfall. As for the possible underestimation of GPP, this is a problem that cannot be resolved without reanalysis of all available data on GPP and NPP.

Appendix A: Aggregation of litter pools

The model adequacy cannot be assessed without due regard to the context within which the model is used. The complexity of a detailed model can be significantly reduced if the model is applied to the ecosystem where the annual mean of the carbon stock in each carbon pool is constant. The carbon flow through the pools can be represented as a stationary Markov chain in such cases. The pools correspond to the states of the Markov chain. The probability of single-step transition from state j to state i is equal to

$$q_{ij} = \frac{f_{ij}}{\sum_{i=1}^n f_{ij}},$$

where f_{ij} is the carbon flow from the j th pool to the i th pool.

The average time that carbon that resides in the j th pool spends in the i th pool before returning to the atmosphere is determined as follows (Logofet and Alexandrov, 1984):

$$t_{ij} = \frac{x_i}{\sum_{j=1}^n f_{ij}} \tilde{q}_{ij},$$

where x_i is the steady-state carbon stock in the i th pool, and \tilde{q}_{ij} is the element of the matrix $(\mathbf{I} - \mathbf{Q})^{-1}$, where \mathbf{I} is the identity matrix and $\mathbf{Q} = (q_{ij})$.

The seasonal depletion of the carbon stock can be significant in the pool, where

$$\frac{x_i}{\sum_{j=1}^n f_{ij}} < 1$$

if the sum of the all inputs to this pool undergoes severe seasonal changes. Such pools can be aggregated into a pool of quickly decaying organic matter, and the other pools can be aggregated into the pool of slowly decaying organic matter with little loss of accuracy.

For example, let us consider the Century model (Parton et al., 1987). The Century model incorporates five pools of carbon: metabolic C, structural C, active soil C, slow soil C, and passive soil C. The residence time of metabolic C is less than 0.5 years. The residence times of other pools are greater than 1.5 years (25 years in the case of slow soil C, and 1000 years in the case of passive soil C). Hence, significant seasonal depletion of carbon stock may occur only in the pool of metabolic C. Other pools may be aggregated into the pool of slowly decaying organic matter. The aggregation will have no effect on the seasonal changes in the heterotrophic respiration from these pools if the monthly rates of decay are proportional to monthly AET:

$$\begin{aligned} R_{h,s}(m) &= \sum_{i=2}^5 \frac{\text{AET}(m)}{\sum_{m=1}^{12} \text{AET}(m)} r_{a,i} s_i = \frac{\text{AET}(m)}{\sum_{m=1}^{12} \text{AET}(m)} \sum_{i=2}^5 r_{a,i} s_i \\ &= \frac{\text{AET}(m)}{\sum_{m=1}^{12} \text{AET}(m)} r_{a,s} s_s, \end{aligned}$$

where

$$s_s = \sum_{i=2}^5 s_i; \quad r_{a,s} = \sum_{i=2}^5 r_{a,i} \frac{s_i}{s_s}.$$

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