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A global model of carbon, nitrogen and phosphorus cycles for the terrestrial biosphere

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Abstract

Carbon storage by many terrestrial ecosystems can be limited by nutrients, predominantly nitrogen (N) and phosphorous (P), in additional to other environmental constraints, water, light and temperature. However the spatial distribution and the extent of both N and P limitation at global scale have not been quantified. Here we have developed a global model of carbon (C), nitrogen (N) and phosphorus (P) cycles for the terrestrial biosphere. Model estimates of steady state C and N pool sizes and major fluxes between plant, litter and soil pools, under present climate conditions, agree well with various independent estimates. The total amount of C in the terrestrial biosphere is 2526 Gt C, and the C fractions in plant, litter and soil organic matter are 21, 6 and 73%. The total amount of N is 124 Gt N, with about 94% stored in the soil, 5% in the plant live biomass, and 1% in litter. We found that the estimates of total soil P and its partitioning into different pools in soil are quite sensitive to biochemical P mineralization that has not been included in any other global models previously. The total amount of P is 26 Gt P in the terrestrial biosphere, 17% of which is stored in the soil organic matter if biochemical P mineralization is modelled, or 40 Gt P, with 60% in soil organic matter, otherwise.

This model was used to derive the global distribution of N or P limitation on the productivity of terrestrial ecosystems. Our model predicts that the net primary productivity of most tropical evergreen broadleaf forests and tropical savannahs is reduced by about 20% on average by P limitation, and most of the remaining biomes are N limited; N limitation is strongest in high latitude deciduous needle leaf forests, and reduces its net primary productivity by up to 40% under present conditions.

1 Introduction

Simulations using global climate models with a fully coupled carbon cycle showed that warming could reduce the net carbon storage in the terrestrial biosphere globally, resulting in an increase in atmospheric (CO_2) concentration and further warming of 0.1 to 1.5°C by 2100 (Friedlingstein et al., 2006). However there are considerable uncertainties in those predictions. For example, none of those models explicitly included nutrient limitations and their responses to climate and higher (CO_2). Both field measurements and theoretical studies have shown that nitrogen limitation can have a significant influence on how the carbon cycle will respond to increasing (CO_2) (Luo et al., 2004) and warming (Medlyn et al., 2000). This is also supported by recent studies using global climate models with carbon and nitrogen cycles (Thornton et al., 2007; Sokolov et al., 2008; Wang and Houlton, 2009).

Globally N and P are the most common nutrients limiting plant growth and soil carbon storage (Vitousek and Howarth, 1991; Aerts and Chapin, 2000). A number of global biogeochemical models have been developed to account for N limitation on the productivity and C uptake by terrestrial biosphere (Parton et al., 1987; McGuire et al., 1995; Thornton et al., 2007; Xu-Ri and Prentice, 2008), but only the CENTURY model (Parton et al., 1987) simulates biogeochemical cycles of C, N and phosphorus (P) and its P cycle submodel has yet to be applied globally. There are some strong reasons why the P cycle should be included in global models for studying the interactions between climate and biogeochemical cycles: (1) both theory and experiments suggest that much tropical forest and savannah are phosphorus limited (Aerts and Chapin, 2000), and tropical forests and savannahs account for about 40% of global vegetation biomass (Saugier, Roy and Mooney, 2001) and 45% of global terrestrial net primary productivity (Field et al., 1998); (2) a recent study by Houlton et al. (2008) showed that biological N fixation, the largest N input to the un-managed terrestrial ecosystems at present is closely related to phosphatase production in the tropics; (3) responses of N and P cycles to climate, increasing atmospheric (CO_2) and human activities can be quite different because of the different biogeochemical controls on N and P cycles in the terrestrial biosphere (Vitousek et al., 1997). For example, the external input to the unmanaged ecosystems is dominated by N fixation for N, but by weathering and dust deposition for P for most unmanaged lands, and loss from the unmanaged ecosystems is dominated by gaseous fluxes via denitrifcation for N and by phosphate leaching for P. Misrepresenting nutrient limitation in the tropics may lead to incorrect predictions under future climate conditions. An early study showed that the relative response of leaf photosynthesis to elevated (CO_2) is smaller when plant growth is P limited (Conroy, et al. 1990) as compared to the response under N-limited conditions and (4) some terrestrial ecosystems may shift from N limitation to P limitation under high N input (Perring et al., 2008) or future climate and higher (CO_2) conditions (Menge and Field, 2007).

Global budgets of N and P, and major biogeochemical fluxes between pools (plant, litter and soil) are quite uncertain (Gruber and Galloway, 2008). For example, the estimate of total P in soil varies from 200 Gt P (Jahnke, 1992) to 41 Gt P (Smil, 2000). The objectives of this study are (1) to construct C, N and P budgets for the terrestrial biosphere for present climate conditions and vegetation distribution using available information of plant biomass, litter fall rate and soil C and N and estimates of P for different soil orders; and (2) to derive a global distribution of N and P limitations, and provide a quantitative estimate of the extent of N and P limitation on plant productivity globally.

In this paper, we describe the development of a global terrestrial biogeochemical model of C, N and P (CASACNP). This model is based on the modified version of the CASA model (Randerson et al., 1996; Fung et al., 2005) and some recent work (Wang et al., 2007; Houlton et al., 2008). Representation of C and N cycles in CASACNP is quite similar to that in CENTURY, but the representation of the P cycle is significantly different. In CASACNP we consider both the biological and biochemical P mineralization (McGill and Cole, 1981), and we find that including biochemical P mineralization in our model has a major impact on the partitioning of soil P in different pools, and therefore the available soil P for plant uptake. In addition, including biochemical P mineralization is important for considering the interaction between the N and P cycles and for modeling N fixation in the future.

In the following, we shall describe the model, and evaluate the model predictions under present climate conditions against independent estimates of various pool sizes and biogeochemical fluxes at global scales. We shall then describe the predicted nutrient limitation globally under the present conditions and discuss possible implications on the responses of the terrestrial biosphere to future climate and CO_2 conditions.

2 Model description

The pools used to represent the C, N and P cycling through the terrestrial ecosystem in plants, litter and soil are shown in Fig. 1. Plants are divided into leaf, wood and root pools, litter into metabolic litter, structural litter and coarse woody debris pools and soil into microbial biomass, slow and passive pools. The turnover rate depends on soil temperature, moisture and texture for litter and soil pools (Randerson et al., 1996) or biome type for plant pools. There is one additional pool for N (inorganic N (NO_3^-+NH_4^+) in the soil) and three additional P pools (labile, sorbed and strongly sorbed P). Change in a pool size with time is governed by a differential equation that is numerically integrated daily. We shall present an overview of each of the three cycles and their interactions in the following sections. A detailed description including key equations and parameter values is given in the appendices. A full list of symbols and their definition are provided in Appendix A.

2.1 Carbon cycle

The carbon cycle is based on CASA' model (Fung et al., 2005). We reduced the number of carbon pools by combining surface litter with soil litter, and surface microbial biomass with soil microbial biomass. This gives three discrete pools in the litter: structural, metabolic and coarse woody debris pools and three organic pools in the soil: microbial biomass, slow and passive pools. The fluxes between different pools are modeled as in CASA'. Details are given in Appendix B.

Transfer coefficients from plant pool i to litter pool j, $b_{j,i}$ and from litter pool j to soil pool k, $c_{k,j}$ are calculated as in CASA' model (see Fung et al., 2005). Turnover rates of litter carbon ($\tau_{L,j}$) or soil carbon ($\tau_{S,k}$) are a function of substrate quality (lignin:N ratio), soil temperature, moisture and soil texture (Randerson et al., 1996). The turnover rate of leaves is calculated as a function of leaf age (Arora and Boer, 2005), and the turnover rates of woody tissue or fine roots are constant for each biome, but vary with biome type (see Table 1).

We used the estimates of monthly NPP by Randerson et al. (1997) ($F_{c,1990}$) multiplying by a biome-specific constant ($x_{np\ \max}$) as the maximal NPP ($F_{c\ \max}$) when nutrients (N or P) are not limiting ($F_{c\ \max}=x_{np\ \max}F_{c,1990}$). The actual net primary production (NPP) depends on leaf N:C ratio ($n_{\mathrm{P,leaf}}$) and P:C ($p_{\mathrm{P,leaf}}$) ratio and the available nutrients (N and P) in the soil. That is

$$F_c = \min\left(\frac{n_{\mathrm{P,leaf}}}{n_{\mathrm{P,leaf}}+k_n}, \frac{p_{\mathrm{P,leaf}}}{p_{\mathrm{P,leaf}}+k_p}\right)\min(x_{n,\mathrm{up}}, x_{p,\mathrm{up}})F_{c\,\max} \tag{1}$$

The first minimum function in Eq. (1) represents the limitation of leaf nutrient concentration on photosynthesis, and the second minimum function represents the nutrient uptake limitation on dry matter production and is equal to 1 at steady state.

We also define the N-limiting factor to NPP ($x_{n,\mathrm{leaf}}$) and P-limiting factor to NPP ($x_{p,\mathrm{leaf}}$) as

$$x_{n,\mathrm{leaf}} = x_{np\,\max}\frac{n_{\mathrm{P,leaf}}}{n_{\mathrm{P,leaf}}+k_n} \tag{2}$$

$$x_{p,\mathrm{leaf}} = x_{np\,\max}\frac{p_{\mathrm{P,leaf}}}{p_{\mathrm{P,leaf}}+k_p} \tag{3}$$

In this study, we assume that k_n=0.01 g N (g C)$^{-1}$ and k_p=0.0006 g P (g C)$^{-1}$. These values are arbitrarily chosen so that NPP is limited by N ($x_{n,\mathrm{leaf}}<x_{p,\mathrm{leaf}}$) when $n_{\mathrm{P,leaf}}/p_{\mathrm{P,leaf}}<16$ (g N/g P) and otherwise NPP is limited by P. In the simulations, we set $x_{n,\mathrm{leaf}}=1$ and $x_{p,\mathrm{leaf}}=1$ if CASACNP is run with the C cycle only, or $x_{p,\mathrm{leaf}}=1$ for C and N cycles only. Under present climate conditions, the estimated pool sizes and fluxes by CASACNP with C, N and P cycles are quite similar to those by CASACNP with C only or with C and N cycles only (<1% differences for pool sizes and <5% for fluxes). This assumes that the model with C cycle, C and N cycles or all three cycles is calibrated under the present climate conditions, and therefore the variables $x_{n,\mathrm{leaf}}$ and $x_{p,\mathrm{leaf}}$ can be considered as the nutrient limitation relative to the present conditions. Values greater than 1 indicate that the nutrient limitation is less than that under present conditions, and vice versa.

The nutrient uptake limiting factors, $x_{n,\mathrm{up}}$ and $x_{p,\mathrm{up}}$ are calculated as

$$x_{n,\mathrm{up}} = \min\left(1, \frac{N_{s,\min}}{F_{n,\mathrm{up}\min}\Delta t}\right) \tag{4}$$

$$x_{p,\mathrm{up}} = \min\left(1, \frac{P_{s,\mathrm{lab}}}{F_{p,\mathrm{up}\min}\Delta t}\right) \tag{5}$$

Where $F_{n,\mathrm{up}\min}$ and $F_{p,\mathrm{up}\min}$ are the amount of minimal N and P uptake required to sustain a given NPP. At steady state, $x_{n,\mathrm{up}}=1$ and $x_{p,\mathrm{up}}=1$. Therefore nutrient uptake does not limit NPP. However when the external environment is changed, such as through an increase in atmospheric (CO_2), the nutrient uptake may limit NPP, and progressive nutrient limitation can occur (Luo et al., 2004).

Parameter $x_{np\ \max}$ is an empirical biome-dependent parameter (>1) (see Table 1) and is tuned so that $F_c=F_{c,1990}$ for each IGBP biome for the 1990s climate and (CO_2).

Because the N:C ratios of litter pools are much lower than those of soil, decomposition of litter can be limited by available soil mineral N. When litter decomposition is not N limited, decomposition of litter and soil is limited by the amount of substrate, not its quality.

When litter or soil carbon is decomposed, some of the decomposed carbon is respired as CO_2. Heterotrophic soil respiration is calculated as the sum of the respired CO_2 from the decomposition of all litter and soil organic C pools. We assumed that the storage change of gaseous CO_2 in the soil is negligible, therefore the surface CO_2 flux is equal to CO_2 production in the soil. The difference between NPP and soil respiration is net ecosystem C exchange (NEE) between the land surface and atmosphere.

Input to the carbon cycle is daily NPP and initial carbon pool size, output are soil respiration, NEE and model pool sizes.

2.2 Nitrogen cycle

The nitrogen cycle is based on the model developed by Parton et al. (1987) and Wang et al. (2007). Similar to the C cycle, the change in N in each pool is governed by a differential equation (see Appendix C). An additional mineral N pool in soil is also represented as only mineral N is assumed to be taken up by plants. We do not include uptake of organic N in soil by roots (Schimel and Bennett, 2004). Ammonia volatilization is not modeled as it usually occurs when soil pH is above 8 (Freney et al., 1983), and the fraction of land with pH>8 is very small globally (Batjes, 1996).

We do not explicitly model the processes of nitrification and denitrification. Therefore our model will need further improvement in the future. In our model gaseous N loss is assumed to be proportional to net N mineralization based on the “hole-in-the-pipe” idea (Firestone and Davidson, 1989) and the rate of leaching loss is proportional to the soil inorganic N pool size. Leaching loss of soil organic matter is not included in our model.

The nitrogen cycle is closely coupled to the carbon cycle; carbon decomposition and gross N mineralization is coupled by the N:C ratios of the substrates (compare Eqs. B2 and B3 with Eqs. C10 and C11). Net N mineralization rate ($F_{n,\mathrm{net}}$) is the difference between gross N mineralization ($F_{n,\mathrm{gr}}$) and N immobilization ($F_{n,\mathrm{im}}$). When net mineralization rate is negative (gross N mineralization<N immobilization), and the additional amount of mineral N required by N immobilization can not be met by the amount of mineral N available, the litter carbon decomposition rate is reduced (see Appendix C Eq. C11 for m_n).

Nitrogen uptake by plants is modeled as a function of soil mineral N pool size, and the demand by plant growth (Eq. C7). The nitrogen demand is a product of maximal

N:C ratio and NPP allocated to each plant pool minus the amount of resorbed N from that pool. When the uptake is less than the minimal demand, NPP is reduced. This is another interaction between the C and N cycles. When the uptake is greater than the minimal demand, the amount of uptake nitrogen allocated to each pool is reduced in proportion to the demand.

During senescence, some fraction of plant tissue nitrogen is resorbed to live tissue, and the remaining goes to the litter pool. Leaf and root litter are partitioned into metabolic litter and structural litter. The N:C ratio is fixed for structural litter (=1/125) but variable for metabolic litter. Woody litter goes to the coarse woody debris pool directly. Only the N:C ratio of soil organic matter and structural litter pools are fixed. N:C ratios of all plant pools are allowed to vary within prescribed ranges.

Input of N to the model includes atmospheric N deposition (both wet and dry), N fertilizer application, N fixation (both symbiotic and asymbiotic) and output includes N leaching and gaseous loss. We used the estimate of N fixation by Wang and Houlton (2009) for the present climate conditions.

2.3 The phosphorus cycle

The phosphorus cycle is based on the model of Wang et al. (2007) and Houlton et al. (2008). The differential equations used to describe the rate of change of each pool are presented in Appendix D. Three differential equations are used to represent the dynamics of labile, sorbed and strongly sorbed phosphorus in soil. The P:C ratio for the three different plant pools can vary within a given range for each biome and the N:P ratios of the newly formed soil organic pools are fixed. However the N:P ratios of the slow and passive pools will change as P in these two pools can be mineralized both biologically and biochemically. The biological P mineralization is the same pathway as N mineralization by microbial activities, and the rate of gross biological P mineralization is calculated as the carbon decomposition rate divided by the P:C ratio of the substrate. P immobilization rate is calculated as the N immobilization rate divided by the N:P ratio of different soil pools. The N:P ratio of the newly formed soil organic pool is 4 g N $(\text{g P})^{-1}$

for microbial biomass and 10 g N $(\mathrm{g\,P})^{-1}$ for the slow and passive pools.

Phosphorus in the slow and passive soil pools can also be mineralized biochemically. Therefore the N:P ratios of the slow and passive pools will increase until a steady state is reached when the P fluxes into those two pools through P immobilization (biologically only) are equal to the rates of P being mineralized (both biologically and biochemically) from those pools. Biochemical mineralization is modeled as a function of soil organic P, the N costs of P uptake and phosphatase production, and maximal specific biochemical P mineralization rate (see Wang et al., 2007; Houlton et al., 2008).

We do not model the biochemical P mineralization of litter P, as turnover rates of the litter pool are much faster than those of the slow and passive soil pools, and all P in the litter will be mineralized biologically if they are not mineralized biochemically within a few years.

We assumed that the labile P pool is equilibrated with the sorbed P within days. The relationship between the amount of labile P and sorbed P is described using the Langmuir equation (Barrow, 1978; Wang et al., 2007). Inputs to the labile P pool are net biological P mineralization and biochemical P mineralization, P weathering, dust deposition and P fertilizer addition. Only labile P can be taken up by plants.

Some of the sorbed P can enter the strongly sorbed P pool that is not exchanged readily with the labile P; the rate of sorbed P to strongly sorbed P is assumed to be proportional to the amount of sorbed P in the soil. The flux from the strongly sorbed P pool to occluded P pool that is not available to plant or soil microbes at a time scale of decades to century is not represented in our model. Including the dynamics of occluded P pool will significantly increase the computation with little impact on the simulated processes we are interested in here at decade or century scales.

Because of the biochemical P mineralization, the P cycle in the soil can become quite decoupled from C and N cycles in the soil (McGill and Cole, 1981). However a recent study by Houlton et al. (2008) showed that the N cycle may be significantly coupled to the P cycle in some tropical soils, as the N fixation is dependent on the rate of biochemical P mineralization and N and P cycles in the N-limited tropical soils can be strongly coupled. Since we do not simulate N fixation explicitly, this coupling between N and P cycle has not yet been included in our present model.

The interaction between the C and P cycles as represented in our model is that NPP is reduced when P uptake is less than the minimal P demand by plants. Inputs of P to the ecosystem are weathering, deposition and fertilizer application. Outputs are the leaching loss of labile P and loss of strongly sorbed P to the occluded P.

2.4 Values of model parameters

The model has a total of 31 pools: 9 C pools, 10 N pools and 12 P pools. The C cycle of the model was calibrated using global data of (CO_2), $^{14}CO_2$ (Randerson et al., 1997; 2002) and used for global studies (Fung et al., 2005). We used the same turnover rates and transfer coefficients for all litter and soil pools as Randerson et al. (1996).

The C:N:P ratios of plant tissues vary within prescribed ranges for each biome based on the results of McGroddy et al. (2004) and Cleveland and Liptzin (2007). C:N ratios of each soil pool and structural litter are fixed, N:C and P:C ratios of the metabolic litter vary, depending on substrate quality. For leaf and root litter with higher N:C, a higher fraction of that litter will enter the metabolic pool. Values of key biome-specific model parameters are listed in Table 1.

Two parameters, $K_{p\,\mathrm{lab}}$ and $S_{p\,\max}$ affect the partitioning between labile P and sorbed P at equilibrium, and the turnover rates of sorbed and strongly sorbed P in the soil also vary with soil order. Based on the estimates of different fractions of labile P, sorbed P and strongly sorbed P for different soil orders by Cross and Schlesinger (1995), we tuned these two parameters for each soil order using a nonlinear parameter estimation technique (Wang et al., 2009).

The biochemical P mineralization rate, $F_{p,\mathrm{tase}}$ affects the model estimate of the fraction of organic P in soil, and is modelled as a function of the maximal specific biochemical P mineralization rate ($v_{p\,\max}$), the N cost of P uptake ($\lambda_{p\,\mathrm{up}}$) and N cost of phosphatase production ($\lambda_{p\,\mathrm{tase}}=15\,\mathrm{g\,N/g\,P}$) (Treseder and Vitousek, 2001). Only $v_{p\,\max}$ is tuned to match the fraction of organic P in soil for each soil order. $\lambda_{p\,\mathrm{up}}$ is 40 g N (g P)$^{-1}$ for tropical evergreen broadleaf forests and savannahs, and is equal to 25 g N (g P)$^{-1}$ for all other biomes (Houlton et al., 2008). These two different values for $\lambda_{p\,\mathrm{up}}$ are chosen to reflect different availability of soil P relative to soil N for plant uptake. For values of other parameters, see Tables 1 and 2.

3 Model integration

The spatial resolution is approximately 220 km globally. We used the dominant IGBP biome type classification under present condition and Zobler soil texture type and USDA soil order within each grid cell (Fig. 2). Fertilizer inputs of N and P are applied uniformly to crop only. Global total amounts of N and P fertilizers applied are 0.08 and 0.015 Gt P year^{-1} (Smil, 2000; Mackenzie, et al., 2002). We used N fixation rates (both symbiotic and asymbiotic) as estimated by Wang and Houlton (2009) for each biome. Spatially explicit estimates of N deposition rate by Dentener (2006) for 1993 and P deposition for 1997 by Mahowald et al. (2008) are used as input. The phosphorous weathering rate was estimated by assigning a constant P weathering rate to each soil order (Table 2) using the soil order map (Fig. 2). The total rate of P weathering we estimated is 0.02 Gt P year^{-1} globally, similar to the estimate of Smil (2000).

The model integration time step is one day. Meteorological inputs required for the model include daily surface air temperature, soil temperature and moisture. The daily meteorological forcing was generated using the CSIRO Conformal Cubic Atmosphere Model, CCAM, (McGregor and Dix, 2008) with the CSIRO Atmosphere and Biosphere Land Exchange (CABLE) land surface scheme (Wang and Leuning, 1998; Kowalczyk et al., 2006) at a spatial resolution of approximately 220 km globally. CCAM was run using six-hourly NCEP reanalysis for 1990 to 1997 (Kalnay et al., 1996) to produce daily mean air temperature, soil temperature and soil moisture in the rooting zone.

By reusing the daily forcings from 1990 to 1997, we ran the model to steady state.

Steady state is considered to have been reached when the relative changes in total pool sizes of C, N or P per land point are less than 0.001% per year. Model outputs are interpolated to a globally uniform 2° by 2° grids over land for comparing with other estimates. All results reported here are for steady state only.

4 Datasets for model evaluation

We used a number of datasets for evaluating the modeled pool sizes and fluxes. These datasets are: global vegetation biomass data (Olsen et al., 1985), soil carbon and nitrogen pool size (Post et al., 1982, 1985), estimates of litter production (Matthews, 1997), atmospheric (CO_2) concentration data (GLOBALVIEW-CO2, 2007) and latitudinal variation of leaf N:P (Hedin, 2004; Reich and Oleksyn, 2004; Kerkhoff et al., 2005).

These datasets are chosen because they are derived either directly from field observations or based on empirical relationships that are estimated from the field observations. Some of the datasets, such as vegetation biomass (Olsen et al., 1985) and litter C production (Matthews, 1997) have spatially explicit information. However, as the biome classifications used by those authors are different from the IGBP biome classification we used in this study, spatially explicit comparisons could be misleading. Instead, we aggregated the spatially explicit estimates by the IGBP biome type, or by latitude for comparing with our estimates. Outputs from other process-based models are not used for evaluations but will be used for comparison. This is because many processes are represented differently in different models, which may result in different pool sizes at steady state.

We did not carry out a rigorous calibration of the model parameters using the above datasets because our preliminary analysis using nonlinear inversion techniques (Wang et al. 2009) showed that the above information is not sufficient to constrain most of the model parameters. In contrast to previous studies (Melillo et al., 1993; Xu-ri and Prentice, 2008), we did not use the measurements from selected sites to calibrate first and then use the calibrated model to study the global responses. Calibrating the model using data from the selected sites may lead to improved model parameter values or model structure for that location, but the values of model parameters may not be representative of a given biome globally.

Atmospheric (CO_2) can be used to provide another independent constraint on the estimated NEE globally (e.g. Randerson et al., 1997). In the northern mid and high latitudes, the seasonal cycle of atmospheric (CO_2) is dominated by the seasonal exchange of carbon between the terrestrial biosphere and atmosphere. Thus correctly modeling the seasonal amplitude of atmospheric (CO_2) is dependent on realistic estimates of the seasonality of NEE (Law et al., 2006). Since here our simulated NPP is tuned to the NPP estimates of Randerson et al. (1997), the ability to match the seasonal cycle of atmospheric (CO_2) tests the seasonality of soil respiration. We evaluate two different functions used for describing the temperature dependence of decomposition. One is the Q10 formulation with a Q10 of 1.72 based on the estimate by Zhou et al. (2009), and the other is the widely used function developed by Kirschbaum (1995) based on the results from soil core studies. Atmospheric (CO_2) is calculated by a linear sum of monthly, regional response functions. Each response function represents the (CO_2) at an observing location due to a month long (CO_2) flux with magnitude of $1\,\mathrm{Pg\,C\,year}^{-1}$. The response functions were calculated using CCAM (McGregor and Dix, 2008) and are the same as those used in Rayner et al. (2008).

5 Results

5.1 Evaluating the equilibrium pool sizes and fluxes

We compared the estimates of vegetation C pools with those by Olsen et al. (1985). Because Olsen et al. (1985) used different biome classification, we calculated land area weighted means of the median, minimum and maximum plant live biomass C for each 2° latitudinal band from their spatially explicit (0.5° by 0.5° globally) estimates. Figure 3a shows that our model vegetation biomass C agrees quite well with the mean of median value by Olsen et al. (1985) at different latitudes except two regions: the tropical region (15° S to 15° N) and southern temperate region (37° S to 45° S). It is important to note here that the median value is only equal to the mean value if the frequency distribution of biomass estimates is normal or uniform. Any deviation of the actual distribution from a normal or uniform distribution may contribute to some of the differences between the two estimates, particularly for latitude bands where land area is small, such as the vegetated land area south of 35° S (see Fig. 3b). In the tropical region, where tropical forest and tropical savanna dominate, our estimated mean biomass C is 13 063 g C m^{-2} for tropical evergreen broadleaf forest and 6220 g C m^{-2} for woody savanna, much higher than the means of median values of 7467 g C m^{-2} and 4029 g C m^{-2} by Olsen et al. (1985), respectively. However our estimated plant live biomass carbon compares well with the estimates of 12 100 g C m^{-2} by Dixon et al. (1994) and 19 428 g C m^{-2} by Saugier, et al. (2001) for tropical evergreen forest. After accounting for the difference in the area of tropical evergreen broadleaf forest used for different studies, the total plant live biomass carbon as estimated by CASACNP is 211 Gt C, similar to the estimates of 212 Gt C by Dixon et al. (1994), 244 Gt C by Ajtay et al. (1979), but much lower than the 340 Gt C by Saugier et al. (2001) for tropical evergreen broadleaf forest using the area from the IGBP vegetation map (see Fig. 2).

In the other region between 37° S and 45° S, our model estimates are closer to the maximal value by Olsen et al. (1985). The mean plant live biomass carbon density as estimated by CASACNP is 4605 g C m^{-2}, much higher than the mean of the median estimate of 2401 g C m^{-2} for the region by Olsen et al. (1985). A relatively small area of land and few field measurements available may contribute to the difference between the median and mean values and the two estimates, as explained earlier. The region is dominated by perennial grasslands (51%) in New Zealand and Argentina (Fig. 2) where there are few estimates of plant live biomass carbon density.

We also compared our estimates of litter productions and coarse woody debris pool sizes for different biomes with other estimates. Matthews (1997) estimated fine and woody litter production for each of 30 biome types. Using her estimates of litter production and the 1° by 1° biome type map of Matthews (1983), we derived the estimates of fine and woody litter productions for each 2° latitudinal band between 60° S to 75° N. For CASACNP, fine litter production is calculated as the sum of litter fall from leaves and roots.

Our estimates of global fine litter production and the total fine litter pool (metabolic and structural litter) are 47 Gt C year^{-1} and 72 Gt C, in good agreement with Matthew's (1997) estimates of 45 to 55 Gt C year^{-1} and 80 Gt C, respectively. Our estimate of fine litter production is more variable with latitude than that of Matthews (1997), particularly in the Southern Hemisphere (Fig. 4). The larger fluctuation of the predicted fine litter production by CASACNP in the Southern Hemisphere is associated with the change in the proportion of the forested land area (Fig. 3b). This regional change in biome type and the impact on fine litter production may not be estimated correctly using the empirical relationship by Matthews (1997); more field studies are needed to verify our estimates.

Estimates of woody litter production by CASACNP agree quite well with those by Matthews (1997) (see Fig. 4). Our estimate of CWD flux is 6.6 Gt C year^{-1} and total CWD pool size is 68 Gt C globally, compared with 6.0 Gt C year^{-1} and 75 Gt C by Matthews (1997). Direct measurements of CWD flux are rare, as it requires successive inventories of the same plots over more than several decades, particularly in old-growth forests (Harmon et al., 1993). Most studies estimate the CWD production using the woody biomass and mortality rate that can be quite sensitive to infrequent disturbance, such as insect attack and extreme weather conditions.

Measurements of total CWD pool sizes are relatively straightforward and more measurements are available. Our estimates of CWD pool sizes for all forest biomes fall within the range of previous estimates. The biome mean CWD pool size we estimated is 2437 g C m^{-2} for evergreen needle forests, 3000 g C m^{-2} for deciduous needle forests, 3762 g C m^{-2} for the temperate and boreal mixed forests, and less than 1000 g C m^{-2} for tropical forests (due to rapid decomposition of woody litter in the tropics). Our estimates are comparable with the estimates compiled by Tang et al. (2003)

for various forests from field measurements. The estimates they compiled vary from 1400 to 5800 g C m^{-2} in coniferous forests and 1380 to 2040 g C m^{-2} in the mixed forest in North America, and 190 to 385 g C m^{-2} for dry tropical forests in Venezuela, and 650 to 8500 g C m^{-2} in tropical rainforests in Chile, Australia and China.

Figure 5 compares estimates of soil organic C, N and C:N ratio by CASACNP with those from Post et al. (1982; 1985). The two estimates agree well with the latitudinal variations of organic C or N in soil organic matter following the change of forested area with latitude (Fig. 3b). This is because the total soil C and N pool sizes of forests are much higher than those of other biome types.

There is no global estimate of total soil P for different biome types. The total amount of soil P is closely related to the property of the parent material and soil age, and the fraction of the soil P available for plant uptake is closely related to soil sorption capacity (Barrow, 1978). To estimate the amount of soil P, we used soil order to distinguish different soil mineralogy and age. Unlike the C and N cycles, most P on land is present in rocks, predominately in apatite. During pedogenesis, the phosphorus in soil parental material is mineralized into soil by weathering and uplift (Porder et al., 2007). Walker and Syers (1976) postulated that the fraction of soil P in the occluded pools unavailable to plants or soil microbes increases as soil ages. This hypothesis is supported by measurements of soil P from sites along chronosequences in Hawaii (Crews et al., 1995) and New Zealand (Johnson et al., 2003; Porder et al., 2007).

Our model estimates that the total P in soil is 40 Gt P if biochemical P mineralization is neglected or 26 Gt P otherwise. Biochemical P mineralization lowers the estimate because it increases the flux from soil organic P to labile P that can be lost by leaching.

Partitioning of soil P into different pools in the soil depends on soil properties, such as sorption capacity and the transfer between different pools. McGill and Cole (1981) emphasized that the cycling of P is quite different from C and N in soil, because P in soil organic matter and litter can be mineralized in two pathways, the biological mineralization through microbial biological activities and biochemical mineralization through phosphatase. Since C and N are only subject to biological mineralization, cycling of

P in soil organic matter can be decoupled from that of C and N. Therefore it is important to consider both biological and biochemical P mineralization for modeling the partitioning of soil P into different pools.

Figure 6 compares our estimates of the fraction of soil P in the soil organic matter, labile, sorbed or strongly sorbed pools with the estimated fractions by Cross and Schlesinger (1995) for different soil orders. Their estimates were based on soil samples collected in the top 15 cm soil, therefore the fractions of different P pools may be quite different from the fractions for the whole rooting zone as in our study. The uncertainties of different fractions as estimated by Cross and Schlesinger (1995) are likely to be large for some soil orders (4, 9 and 12 in Fig. 6), as only a few measurements (<3) were available.

Our model with biochemical P mineralization estimates total soil P fractions of 17, 4, 37 and 41 in the soil organic matter, labile, sorbed and the strongly sorbed pools, compared to 17, 6, 43 and 34% from Cross and Schlesinger (1995) for the top 15 cm soil and the USDA soil order maps. The major difference between the two estimates is the higher fraction of P in the strongly sorbed P pool. Some of the difference may be because the soil P we modeled is for the entire rooting zone, as compared with the top 15 cm for the data compiled by Cross and Schlesinger (1995). More field measurements of biochemical P mineralization are needed, particularly for some undersampled soil orders and deeper soil (>15 cm).

Figure 6 also compares the modelled P fractions of different soil pools with or without biochemical P mineralization in the soil. Without biochemical P mineralization, the modelled fraction of P in soil organic matter accounts for over 50% of total soil P for all soil orders, and the fractions of labile P are <2% and the fractions of the sorbed P <25%. While the fraction of labile P in soil can vary during the growing season (Townsend et al. 2007), the fraction of P in soil organic matter is usually less than one third of total P for most soils except some highly weathered soil in the tropics (Cross and Schlesinger, 1995) when biochemical P mineralization is considered. Consequently including biochemical P mineralization is very important for correctly representing soil

P dynamics.

5.2 Comparison with atmospheric (CO_2) measurements

Response functions have been used to reconstruct the atmospheric (CO_2) at 59 sites, given the steady-state carbon fluxes from CASACNP. Two sets of carbon fluxes have been used, differing only in the choice of temperature dependence of litter and soil decomposition. Overall the seasonal cycle of atmospheric (CO_2) is well simulated by the Q10 option but shows too little seasonality when the Kirschbaum (1995) formulation is used. Figure 7 shows the difference between the simulated and observed (GLOBALVIEW-CO2, 2007) peak-to-peak amplitude of the seasonal cycle. In the Q10 case, the differences are close to zero for most sites while the differences in the Kirschbaum case are all negative; the Kirschbaum simulated amplitudes are typically less than half the magnitude of the observed amplitudes. In the Q10 case two Northern Hemisphere sites show amplitudes that are overestimated by greater than 50%: Fraserdale (Canada) and Ulaan Uul (Mongolia). Both are mid-continental sites and may be susceptible to local flux errors. The response function reconstruction is also less reliable for continental sites which have large diurnal cycles. By contrast, the amplitudes are very well simulated at remote sites such as Mauna Loa, Hawaii and Alert, Canada, where the air masses are well-mixed.

5.3 Global nutrient limitation to net primary productivity

Nitrogen and phosphorus are the two most common nutrients limiting plant productivity (Vitousek and Howarth, 1991; Koerselman and Mueleman, 1996). It has been suggested that NPP is N limited when leaf N:P (on mass basis) <14 and is P limited when leaf N:P>16 based on broad-scale geographic variations of leaf N:P ratios (Koerselman and Mueleman, 1996). Figure 8 shows that the modeled leaf N:P ratios by CASACNP agree quite well with some empirical relationships derived from field observations. Our results show that productivity of most biomes in the tropics is P limited while the productivity of temperate and boreal forests is N-limited. However there is considerable variability within each latitudinal band.

Figure 9 shows the variations of leaf N:C and P:C ratios and the nutrient limitation factor for all land points not covered by snow and ice permanently. Leaf N:C ratios of tropical forests, savannah and crop land vary between 0.04 to 0.05 g N $(\mathrm{g\,C})^{-1}$, and are significantly higher than other biome types. N:C ratio is lowest in the deciduous needle leaf forests in the boreal region, varying between 0.015 and 0.02 g N $(\mathrm{g\,C})^{-1}$. The leaf P:C ratio varies between 0.001 and 0.003 g P $(\mathrm{g\,C})^{-1}$ for unmanaged biome types, and is about 0.004 g P $(\mathrm{g\,C})^{-1}$ for crop land.

Figure 9 also shows that the NPP of tropical evergreen forest and savannah and some crop land in the USA, Asia and Australia is limited by P. Most other biomes are limited by N. The deciduous needle forests and high latitude shrub lands (or tundra) are most strongly limited by N.

Our results agree broadly with results from a recent synthesis by LeBauer and Treseder (2008), who showed that nitrogen limitation is widespread and the relative increase in NPP in response to N fertilizer application varies from 11% for desert ecosystems to 35% in the tundra, with a global mean response of 29%. For the N-limited biomes, we estimate that N limitation reduces NPP by 10 to 40% under the present climate and (CO_2).

LeBauer and Treseder (2008) also showed that N fertilizer addition would increase the NPP of tropical forests by about 20%, whereas our results show that nearly all tropical forests are P limited and will therefore not respond to N fertilizer addition. This discrepancy can be explained by two factors: the first one is that our model only captures the broad variations of nutrient limitation because of the relatively coarse resolution (2° by 2°); some fine-scale variations of leaf N:P ratio and limiting nutrients are not well captured by our model simulation. For example, it has been observed that leaf N:P ratios and available soil N or P are quite variable in space and time in the tropical forests in South America (Townsend et al. 2007). The second factor is that N addition may increase biochemical P mineralization and therefore will increase NPP even when

NPP is P-limited (Houlton et al. 2008). To represent this connection between N and P cycles in soil, we need to model the N cost of P uptake and N fixation explicitly.

6 Discussion

6.1 Major carbon, nitrogen and phosphorus pool sizes, fluxes and comparison with other estimates

Global budgets of C, N and P and major fluxes between plant, litter and soil are constructed for the present climate and (CO_2) level (see Fig. 10). The global mean C:N:P ratio on mass basis is 1648:20:1 for plant live biomass, and 2333:20:1 for litter and 72:5:1 for soil in the terrestrial biosphere.

Our estimate of total plant live biomass C is much higher than the median estimate of 427 Gt C by Olsen et al. (1985), but similar to the estimate of 560 Gt C by Ajtay et al. (1979) and of 652 Gt C by Saugier et al. (2001). Our estimate of soil carbon of 1846 Gt C is for the entire rooting zone within which the root biomass density decreases with soil depth (see Jackson et al., 1996), and is therefore much higher than the estimate of 1500 Gt C of Post et al. (1982) for the top 1 cm soil, but quite close to the estimate of 2300 Gt C for the top 3 m by Batjes (1996) for soil carbon. Overall our estimate of plant live biomass carbon shows two large peaks, one being in the tropics (15° S to 15° N) and the other being in the temperate and boreal region (50° N to 65° N). These regions account for 38 and 20% of total plant live biomass carbon. The NPP is limited by available soil P for the tropical peak, but by available soil N for the temperate and boreal peak.

Few estimates of total N in pools are available for the global terrestrial biosphere. Xu-ri and Prentice (2008) estimated that the total amount of N is 5.6 Gt N in plants, 3.2 Gt N in litter and 56.8 Gt N in soil using their model. Their soil N estimate is much lower than our estimate of 116 Gt N in the soil. Our estimate of soil N is between the 100 Gt N by Post et al. (1985) for the top 1 m soil and 156 Gt N by Batjes (1996) for the top 3 m of soil globally.

Estimates of P in the terrestrial biosphere are few, and quite variable (Jahnke, 1992; Smil, 2000; Mackenzie et al., 2002). Most measurements of soil P were made on available P that only accounts for 3 to 10% of total soil P in agricultural soils, and measurements on forest soil are relatively scarce. As a result, estimates of total soil P vary from 40 Gt P (Smil, 2000) to 200 Gt P (Jahnke, 1992).

Smil (2000) pointed out that the early estimate of total soil P by Jahnke (1992) was too high, and she estimated the amount of P in soil to be 5 to 10 Gt P in organic forms and 35 to 40 Gt P in inorganic forms. Mackenzie et al. (2002) estimated that the total organic P is only about 5 Gt P globally, similar to our estimate of 4.4 Gt P in soil organic matter and 21.1 Gt P in the labile, sorbed and strongly sorbed pools globally. Assuming that the average amount of occluded P is 15% of total P globally (Johnson et al., 2003), we estimate that the total amount of occluded P is 4.6 Gt P, and total soil P will be 30.6 Gt P, close to the lower estimate by Smil (2000).

Previous studies estimated that the total amount of P in terrestrial plants varies between 0.5 to 3 Gt P (Jahnke, 1992; Smil, 2000). Given the amount of N in total terrestrial plant live biomass is 6.7 Gt N, and the N:P ratio can vary from 10 to 20 g N $(\mathrm{g\,P})^{-1}$ in plants (Vitousek, 1984, 2004), we conclude that the estimate of 3 Gt P in plant live biomass is too high unless we underestimate the total amount of N in plant live biomass by an order of magnitude. On the contrary we may have overestimated the amount of N in plants, as the C:N ratios we used are relatively low, compared with some other estimates (for example, Vitousek, 1984, 2004).

At steady state, the total carbon flux from plant to litter is equal to NPP, and is equal to soil respiration. The NPP we used is 53 Gt C year^{-1}. N inputs to the terrestrial biosphere include N fixation (both symbiotic and asymbiotic) of 0.142 Gt N year^{-1} (see Wang and Houlton, 2009), N deposition is 0.069 Gt N year^{-1} for 1990's (Dentener, 2006), and fertilizer N addition of 0.086 Gt N year^{-1} (Galloway et al., 2004). The total N loss rate from soil is 0.295 Gt N year^{-1}. Total plant N uptake is equal to net N mineralization, and is 1.1 Gt N year^{-1}, similar to the estimate of 1 Gt N year^{-1} by McGuire et al. (1995) and Xu-ri and Prentice (2008). We also estimated that the annual N loss is 0.06 Gt N year^{-1}, which is quite similar to the estimated total export of N from land to river and coastal oceans of 0.07 Gt N year^{-1} (Seitzinger et al., 2006). Our estimate of total N gaseous loss is 0.237 Gt N year^{-1}, and is 1.9 times the global soil denitrification rate of 0.124 Gt N year^{-1} as estimated by Seitzinger et al. (2006). Some of the difference between the two estimates may result from N gaseous losses from nitrification and asymbiotic N fixation that are not accounted for by Seitzinger et al. (2006).

The total input of P to the terrestrial biosphere is 0.036 Gt P year^{-1}; P weathering, inorganic P fertilizer addition and dust P deposition account for 56, 42 and 2% of the total input, respectively. The rate of P loss by leaching is estimated to be 0.026 Gt P year^{-1}, and about 0.01 Gt P year^{-1} is transferred to the occluded P pools with a residence time>100 years, the rest (0.016 Gt P year^{-1}) was lost by leaching. Using nutrient data from major rivers and coastal regions and water fluxes, Seitzinger et al. (2006) estimated the total P lost to the river and coastal ocean is 0.01 Gt P year^{-1}.

The mean residence at steady state can be calculated as the ratio of pool sizes and influx for C, N and P in plant, litter and soil. The total mean residence time in the terrestrial biosphere is 47 years for C, 425 years for N and 722 years for P, which is considerably longer than the mean residence time of each individual pool (Fig. 10). For nutrients N and P, the exchange fluxes between plant, litter and soil within the terrestrial biosphere are much larger than the external flux into the terrestrial biosphere, therefore internal cycling of the nutrients dominates the cycling of N and P, as compared with the C cycle. The mean residence time constants of N and P in plants or litter are quite similar for N and P, but much shorter than the respective mean residence time of C, as a result of nutrient resorption by plants.

Human activities have had a significant impact on nutrient cycling (Vitousek et al., 1997; Gruber and Galloway, 2008). This is also evident in Fig. 10. Fertilizer applications account for 27% of total N input and 42% of total P input to the terrestrial biosphere, or 1% of total plant N uptake and 25% of total plant P uptake.

As carbon uptake by the terrestrial biosphere can be limited by nutrients, models that do not consider nutrient limitation explicitly will give biased estimates of carbon uptake under future climate and (CO_2) conditions, as shown by Thornton et al. (2007) and Sokolov et al. (2008). For biomes at high latitude where nutrient mineralization is temperature limited, warming will increase nutrient mineralization and nutrient availability, therefore the carbon – climate feedback will be much lower than the estimates by models without nutrient limitation. For tropical forests and savannah, carbon uptake is limited by P, and the response of NPP to increasing (CO_2) will be much lower if the measured response in the laboratory is extrapolated to the field. The significance of P limitations on the response of terrestrial C storage to global climate change and future (CO_2) and feedback between nutrients (N and P) and climate is yet to be demonstrated at regional or global scales. We are implementing CASACNP into a global climate model to address this issue.

7 Conclusions

We developed a global model of C, N and P cycle for the terrestrial biosphere. Estimates of C, N and P pool sizes and major fluxes between plant, litter and soil agree well with various independent estimates. Our estimate of total soil P is much smaller than the earlier estimate of 200 Gt P that is quite widely quoted in the literature.

Including biochemical P mineralization is important for modeling the P cycle in the terrestrial ecosystem. If biochemical P mineralization is not accounted for, the model will overestimate the fraction of soil organic P and underestimate the fractions of P in the labile, sorbed and strongly sorbed pools, and the dynamics of soil P incorrectly.

Using our model for the present climate conditions, we derived the first spatially explicit estimates of nutrient (N and P) limitation globally. Our result shows that most tropical forest and savannahs are P-limited, and their net primary productivities are reduced by 20% due to P limitation. Most of the remaining vegetations is N-limited, and N limitation is strongest in the deciduous needle leaf forest at the high latitudinal regions of the Northern Hemisphere, and N limitation reduces its NPP by about 40%.

Appendix A List of symbols and their definitions

The subscript *i* is for different plant pools leaf, wood or root, and *j* for different litter pools, metabolic litter, structural litter or coarse woody debris, *k* or *kk* for different soil pools, microbial biomass, slow pool or passive pool.

A1 State variables

$C_{P,i}$: amount of carbon in a plant pool *i* ($\mathrm{g\,C\,m^{-2}}$).

$C_{L,j}$: amount of carbon in a litter pool *j* ($\mathrm{g\,C\,m^{-2}}$).

$C_{S,k}$: amount of carbon in a soil pool *k* ($\mathrm{g\,C\,m^{-2}}$).

$N_{P,i}$: amount of nitrogen in a plant pool *i* ($\mathrm{g\,N\,m^{-2}}$).

$N_{L,j}$: amount of nitrogen in a litter pool *j* ($\mathrm{g\,N\,m^{-2}}$).

$N_{S,k}$: amount of nitrogen in a soil organic pool *k* ($\mathrm{g\,N\,m^{-2}}$).

$N_{S,\mathrm{min}}$: amount of mineral N in soil ($\mathrm{g\,N\,m^{-2}}$).

$P_{P,i}$: amount of phosphorus in a plant pool *i* ($\mathrm{g\,P\,m^{-2}}$).

$P_{L,j}$: amount of phosphorus in a litter pool *j* ($\mathrm{g\,P\,m^{-2}}$).

$P_{S,k}$: amount of phosphorus in a soil organic pool *k* ($\mathrm{g\,P\,m^{-2}}$).

$P_{S,\mathrm{lab}}$: amount of phosphorus in the labile soil pool ($\mathrm{g\,P\,m^{-2}}$).

$P_{S,\mathrm{sorb}}$: amount of phosphorus in the sorbed soil pool ($\mathrm{g\,P\,m^{-2}}$).

$P_{S,\mathrm{ssb}}$: amount of phosphorus in the strongly sorbed soil pool ($\mathrm{g\,P\,m^{-2}}$).

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A2 Model parameters

a_i: biome-specific fraction of NPP allocated to plant pool i during steady leaf growth.

$f_{n\,\mathrm{gas}}$: fraction of net nitrogen mineralization rate that is lost to the atmosphere (=0.05).

$f_{n\,\mathrm{leach}}$: fraction of soil mineral N that is lost by leaching (fraction) (0.5 year^{-1}).

f_p: fraction of labile P lost by leaching (=0.04 year^{-1}).

k_n: an empirical parameter for nitrogen limitation on NPP (=0.01 g N/g C).

k_p: an empirical parameter for phosphorus limitation on NPP (=0.0006 g P/g C).

$n_{P\,\max,i}$: biome-specific maximal N:C ratio of a plant pool i (g N/g C).

$n_{P\,\min,i}$: biome-specific minimal N:C ratio of a plant pool i (g N/g C).

$n_{S,k}$: biome-specific N:C ratio of soil organic pool k (g N/g C).

$p_{P\,\max,i}$: biome-specific maximal P:C ratio of a plant pool i (g P/g C).

$p_{P\,\min x,i}$: biome-specific minimal P:C ratio of a plant pool i (g P/g C).

$r_{n,i}$: nitrogen resorption coefficient of plant pool i (=0.5 for leaf, =0.9 for wood and root).

$r_{p,i}$: phosphorus resorption coefficient of plant pool i (=0.5 for leaf, =0.9 for wood and root).

$v_{p\,\max}$: biome-specific maximal specific rate of biochemical P mineralization (year^{-1}).

$x_{np\,\max}$: a biome-dependent empirical parameter (dimensionless).

$K_{\mathrm{N,up}}$: an empirical parameter relating plant nitrogen uptake rate to soil mineral N amount (=2 g N m^{-2}).

$K_{\mathrm{P,up}}$: an empirical parameter relating plant P uptake rate to labile P pool size in the soil (=0.5 g P m^{-2})

$K_{p\,\mathrm{lab}}$: an empirical parameter for describing the equilibrium between labile P and sorbed ($\mathrm{g\,P\,m^{-2}}$).

$K_{p\,\mathrm{tase}}$: an empirical parameter (=150 g N/g P).

$S_{p\ \max}$: maximum amount of sorbed P ($\mathrm{g\,P\,m^{-2}}$) ($\mathrm{g\,P\,m^{-2}}$).

$\tau_{P,\mathrm{sorb}}$: rate constant for sorbed P (=0.01 $\mathrm{year^{-1}}$).

$\tau_{P,\mathrm{ssb}}$: rate constant for strongly sorbedP (=0.01 $\mathrm{year^{-1}}$).

$\lambda_{p\,\mathrm{up}}$: N cost of P uptake (=40 g N/g P for tropical biomes and =25 g N/g P for other biomes).

$\lambda_{p\,\mathrm{tase}}$: biome-specific N cost of phosphatase production (=15 g N/g P).

A3 Fluxes

F_c: net primary productivity (g C m^{-2} year^{-1}).
$F_{c,1990}$: net primary productivity for 1990's (g C m^{-2} year^{-1})
$F_{c,\mathrm{max}}$: maximal net primary productivity (g C m^{-2} year^{-1}).
$F_{n,\mathrm{dep}}$: atmospheric nitrogen deposition rate (g N m^{-2} year^{-1}).
$F_{n,\mathrm{fix}}$: nitrogen fixation rate (g N m^{-2} year^{-1}).
$F_{n,\mathrm{fert}}$: nitrogen fertilizer addition rate (g N m^{-2} year^{-1}).
$F_{n,\mathrm{gr}}$: gross nitrogen mineralization rate (g N m^{-2} year^{1}).
$F_{n,\mathrm{im}}$: nitrogen immobilization rate (g N m^{-2} year^{-1}).
$F_{n,\mathrm{net}}$: nitrogen net mineralization rate (g N m^{-2} year^{-1}).
$F^*_{n,\mathrm{net}}$: net N mineralization rate when decomposition is not N-limited (g N m^{-2} year^{-1}).
$F_{n,\mathrm{up}}$: plant nitrogen uptake rate (g N m^{-2} year^{-1}).
$F_{n,\mathrm{up\,min}}$: minimum nitrogen uptake rate by plants (g N m^{-2} year^{-1}).
$F_{n,\mathrm{loss}}$: rate of nitrogen loss from soil (g N m^{-2} year^{-1}).
$F_{P,\mathrm{dep}}$: P deposition rate (g P m^{-2} year^{-1}).
$F_{P,\mathrm{net}}$: net biological P mineralization rate (g P m^{-2} year^{-1}).
$F_{P,\mathrm{fert}}$: P fertilizer addition rate (g P m^{-2} year^{-1}).
$F_{\mathrm{P,up}}$: plant P uptake rate (g P m^{-2} year^{-1}).
$F_{n,\mathrm{up\,min}}$: minimum phosphorus uptake rate by plants (g P m^{-2} year^{-1}).
$F_{P,\mathrm{loss}}$: soil P loss rate (g P m^{-2} year^{-1}).
$F_{p,\mathrm{tase}}$: biochemical P mineralization rate (g P m^{-2} year^{-1}).

A4 Other variables

$a_{c,i}$: Fraction of NPP allocated to plant pool i (fraction).

$a_{n,i}$: fraction of plant nitrogen uptake allocated to a plant pool i (fraction).

$a_{p,i}$: fraction of plant phosphorus uptake allocated to a plant pool i (fraction).

$b_{j,i}$: fraction of litter from plant pool i allocated to litter pool j (fraction).

$c_{k,j}$: fraction of carbon from litter pool j allocated to soil pool k (fraction).

$d_{k,kk}$: fraction of carbon from soil pool kk to another soil pool k (fraction).

m_n: nitrogen limitation on litter C decomposition (dimensionless).

$n_{L,j}$: N:C ratio of litter pool j (g N/g C).

$n_{P,i}$: N:C ratio of plant pool i (g N/g C).

$n_{P\ \mathrm{min},i}$: minimal N:C ratio of a plant pool i (g N/g C).

$n_{P\ \mathrm{max},i}$: maximal N:C ratio of a plant pool i (g N/g C).

$p_{L,j}$: P:C ratio of litter pool j (g P/g C).

$p_{P,i}$: P:C ratio of plant pool i (g P/g C).

$p_{S,k}$: P:C ratio of soil organic pool k (g P/g C).

t: time in day

$x_{n,\mathrm{leaf}}$: leaf nitrogen limitation on NPP (dimensionless).

$x_{p,\mathrm{leaf}}$: leaf phosphorus limitation on NPP (dimensionless).

$x_{n,\mathrm{up}}$: nitrogen uptake limitation on NPP (dimensionless).

$x_{p,\mathrm{up}}$: phosphorus uptake limitation on NPP (dimensionless).

x_{npmax}: ratio of the maximal NPP and NPP in 1990's for each biome (dimensionless).

$\tau_{P,i}$: turnover rate of a plant pool i (year^{-1}).

$\tau_{L,j}$: turnover rate of a litter pool j (year^{-1}).

$\tau_{S,k}$: turnover rate of a soil pool k (year^{-1}).

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Appendix B The carbon cycle

There are nine carbon pools in the model. The equations governing the change of C pools are:

$$\frac{dC_{P,i}}{dt} = a_{c,i}F_c - \tau_{P,i}C_{P,i}\,, \quad i = \text{leaf, wood or root}; \tag{B1}$$

$$\frac{dC_{L,j}}{dt} = \sum_i b_{j,i}\tau_{P,i}C_{P,i} - m_n\tau_{L,j}C_{L,j}\,, \quad j = \text{met, str or cwd}; \tag{B2}$$

$$\frac{dC_{S,k}}{dt} = \sum_j c_{k,j}m_n\tau_{L,j}C_{L,j} + \sum_{kk} d_{k,kk}\tau_{S,kk}C_{S,kk} - \tau_{S,k}C_{S,k}\,, \quad k \neq kk; \tag{B3}$$

and k or kk=mic, slow or pass.

where C denotes pool size in g C m^{-2} and τ turnover rate in year^{-1}, they both have two subscript, the first subscript is P for plant, L for litter or S for soil, the second subscript for different pools in plant, litter or soil. $a_{c,i}$ is the fraction of NPP (F_c) allocated to plant pool i, $b_{j,i}$ is the fraction of litter fall from a plant pool i allocated to litter pool j, and $c_{k,j}$ is the fraction of litter carbon that enters soil pool k, and $d_{k,kk}$ is the fraction of decomposed C from soil pool kk to soil pool k, m_n is the N limitation on litter decomposition (see Eq. C12), and varies from 0 to 1.

Coefficient $a_{c,j}$ is the fraction of NPP allocated to leaf, wood or root. It depends on leaf phenology. Leaf phenology is derived from the estimates of remote sensing observations (Zhang, Friedle and Schaaf, 2006). Leaf growth is divided into four phases separated by the onset of leaf bud burst, steady leaf growth and leaf senescence. Phase 1 starts from leaf budburst to the start of steady leaf growth, phase 2 starts from the beginning of steady leaf growth to the beginning of leaf senescence, phase 3 represents the period of leaf senescence and phase 4 starts from the end of leaf senescence to the start of leaf bud burst.

During steady leaf growth, the allocation coefficients are constant but vary from biome to biome. That is: $a_{c,\mathrm{leaf}}=a_{\mathrm{leaf}}$, $a_{c,\mathrm{wood}}=a_{\mathrm{wood}}$ and $a_{c,\mathrm{root}}=a_{\mathrm{root}}$. During phases 3 and 4, allocation to leaf is set to zero, and the value of a_{leaf} is added to $a_{c,\mathrm{wood}}$ and $a_{c,\mathrm{root}}$ in proportional to a_{wood} and a_{root}, respectively. During phase 1, $a_{c,\mathrm{leaf}}$ is set to 0.8, $a_{c,\mathrm{wood}}$ and $a_{c,\mathrm{root}}$ both are set to 0.1 for woody biomes, and $a_{c,\mathrm{wood}}=0$ and $a_{c,\mathrm{root}}=0.2$ for non-woody biomes.

Leaf mortality will increase with cold and drought stress, and is modeled following the approach of Arora and Boer (2005). The partitioning coefficient, $b_{j,i}$, $c_{k,j}$, $d_{k,kk}$, $\tau_{L,j}$ and $\tau_{S,k}$ use the same values as in CASA model (see Randerson et al., 1996).

Appendix C The nitrogen model

There are nine organic N pools and one inorganic soil N pool. The equations governing N pool dynamics are:

$$\frac{dN_{P,i}}{dt} = a_{n,i}F_{n,\mathrm{up}} - \tau_{P,i}(1-r_{n,i})N_{P,i} \tag{C1}$$

$$\frac{dN_{L,\mathrm{str}}}{dt} = (b_{\mathrm{str,leaf}}\tau_{\mathrm{P,leaf}}C_{\mathrm{P,leaf}} + b_{\mathrm{str,root}}\tau_{\mathrm{P,root}}C_{\mathrm{P,root}})n_{L,\mathrm{str}} - m_n\tau_{L,\mathrm{str}}N_{L,\mathrm{str}} \tag{C2}$$

$$\begin{aligned}\frac{dN_{L,\mathrm{met}}}{dt} &= \tau_{\mathrm{P,leaf}}(1-r_{n,\mathrm{leaf}})N_{\mathrm{P,leaf}} + \tau_{\mathrm{P,root}}(1-r_{n,\mathrm{root}})N_{\mathrm{P,root}} \\ &\quad -(\tau_{\mathrm{P,leaf}}C_{\mathrm{P,leaf}} + \tau_{\mathrm{P,root}}C_{\mathrm{P,root}})n_{L,\mathrm{str}} - m_n\tau_{L,\mathrm{str}}N_{L,\mathrm{str}}\end{aligned} \tag{C3}$$

$$\frac{dN_{L,\mathrm{cwd}}}{dt} = \tau_{P,\mathrm{wood}}N_{P,\mathrm{wood}} - m_n\tau_{L,\mathrm{cwd}}N_{L,\mathrm{cwd}} \tag{C4}$$

$$\frac{dN_{S,k}}{dt} = \sum_j c_{k,j}m_n\tau_{L,j}N_{L,j} + \sum_{kk} d_{k,kk}\tau_{S,kk}N_{S,kk} - \tau_{S,k}N_{S,k}\,, \quad k \neq kk \tag{C5}$$

$$\frac{dN_{S,\text{min}}}{dt} = F_{n,\text{dep}} + F_{n,\text{fix}} + F_{n,\text{fert}} + F_{n,\text{net}} - F_{n,\text{up}} - F_{n,\text{loss}} \tag{C6}$$

where N is the N pool size, $a_{n,i}$ is the allocation of N uptake to different plant pools, $F_{\text{N,up}}$ is the root N uptake ($\text{g N m}^{-2}\,\text{d}^{-1}$), $r_{n,i}$ the N resorption coefficient, $n_{L,\text{str}}$ is the N:C ratio of structural litter pool ($=1/125\,\text{g N (g C)}^{-1}$), $F_{n,\text{dep}}$, $F_{n,\text{fix}}$, $F_{n,\text{fert}}$, $F_{n,\text{net}}$ and $F_{n,\text{loss}}$ are the N deposition rate, fixation rate, fertilizer N addition rate, net N mineralization rate and N loss rate, all are in $\text{g N m}^{-2}\,\text{year}^{-1}$.

Uptake of N by plant from soil, $F_{n,\text{up}}$ is calculated as

$$F_{n,\text{up}} = \sum_i \left(a_{c,i}F_c(n_{P\,\text{max},i} - n_{P\,\text{min},i}) - r_{n,i}\tau_{P,i}N_{P,i}\right)\frac{N_{S,\text{min}}}{N_{S,\text{min}} + K_{\text{N,up}}} + F_{n,\text{up}\,\text{min}} \tag{C7}$$

where $n_{P\,\text{min},i}$ and $n_{P\,\text{max},i}$ are the minimal and maximal N:C ratios of plant pool i, $K_{\text{N,up}}$ is an empirical constant ($=2\,\text{g N m}^{-2}$). $F_{n,\text{up}\,\text{min}}$ the minimal N uptake for a given NPP and is calculated as

$$F_{n,\text{up}\,\text{min}} = \sum_i \left(a_{c,i}F_c n_{P\,\text{min},i} - r_{n,i}\tau_{P,i}N_{P,i}\right) \tag{C8}$$

Allocation of the N uptake among different plant pools, $a_{n,i}$ is calculated to be in proportional to the demand of N by pool i. That is

$$a_{n,i} = \frac{\left(a_{c,i}F_c(n_{P\,\text{max},i} - n_{P\,\text{min},i}) - r_{n,i}\tau_{P,i}N_{P,i}\right)\frac{N_{S,\text{min}}}{N_{S,\text{min}}+K_{\text{N,up}}} + \left(a_{c,i}F_c n_{P\,\text{min},i} - r_{n,i}\tau_{P,i}N_{P,i}\right)}{F_{n,\text{up}}} \tag{C9}$$

Net N mineralization rate is calculated as the difference of gross N mineralization ($F_{n,\text{gr}}$) and N immobilization ($F_{n,\text{im}}$) rate. Gross N mineralization rate, $F_{n,\text{gr}}$ is calculated as

$$F_{n,\text{gr}} = \sum_j m_n\tau_{L,j}N_{L,j} + \sum_k \tau_{S,k}N_{S,k} \tag{C10}$$

N immobilization rate, $F_{n,\mathrm{im}}$, is calculated as

$$F_{n,\mathrm{im}} = \sum_{k} \sum_{j} m_n c_{k,j} \tau_{L,j} N_{L,j} + \sum_{k} \sum_{kk} d_{k,kk} \tau_{S,kk} N_{S,kk} \quad k \neq kk \tag{C11}$$

The N-limiting factor on litter decomposition, m_n, is calculated as

$$m_n = \begin{cases} 1; & F^*_{n,\mathrm{net}} > 0 \\ \max\left(0, 1 + \frac{F^*_{n,\mathrm{net}} \Delta t}{N_{s,\min}}\right) & F^*_{n,\mathrm{net}} \leq 0 \end{cases} \tag{C12}$$

Where $F^*_{n,\mathrm{net}}$ is the net N mineralization rate when decomposition is not N-limited, and is calculated as

$$F^*_{n,\mathrm{net}} = \sum_{k} \sum_{j} (1 - c_{k,j}) \tau_{L,j} N_{L,j} + \sum_{k} \sum_{kk} (1 - d_{k,kk}) \tau_{S,kk} N_{S,kk} \quad k \neq kk \tag{C13}$$

Two pathways of N losses are modeled. One is gaseous loss and the other is leaching. Gaseous N loss is proportional to net N mineralization (see Firestone and Davidson, 1989) and leaching loss is proportional to the mineral N pool. That is

$$F_{n,\mathrm{loss}} = f_{n\,\mathrm{gas}} F_{N,\mathrm{net}} + f_{n\,\mathrm{leach}} N_{S,\min} \tag{C14}$$

where $f_{n\,\mathrm{gas}}$ is equal to 0.05 (see Parton et al., 1987) and $f_{n\,\mathrm{leach}}$ is equal to 0.5 year^{-1} (see Hedin, Armesto and Johnson, 1995).

Appendix D Phosphorus cycle

There are 12 P pools. Equations governing the dynamics of P pools are:

$$\frac{dP_{P,i}}{dt} = a_{p,i} F_{p,\mathrm{up}} - \tau_{P,i} (1 - r_{p,i}) P_{P,i} \tag{D1}$$

$$\frac{dP_{L,\mathrm{str}}}{dt} = \left(b_{\mathrm{str,leaf}} \tau_{\mathrm{P,leaf}} C_{\mathrm{P,leaf}} + b_{\mathrm{str,root}} \tau_{\mathrm{P,root}} C_{\mathrm{P,root}}\right) p_{L,\mathrm{str}} - m_n \tau_{L,\mathrm{str}} P_{L,\mathrm{str}} \tag{D2}$$

$$\frac{dP_{L,\mathrm{met}}}{dt} = \tau_{\mathrm{P,leaf}}\left(1-r_{p,\mathrm{leaf}}\right)P_{\mathrm{P,leaf}} + \tau_{P,\mathrm{root}}\left(1-r_{p,\mathrm{root}}\right)P_{\mathrm{P,root}} - \left(\tau_{\mathrm{P,leaf}}C_{\mathrm{P,leaf}} + \tau_{\mathrm{P,root}}C_{\mathrm{P,root}}\right)p_{L,\mathrm{str}} - m_n\tau_{L,\mathrm{str}}P_{L,\mathrm{str}} \tag{D3}$$

$$\frac{dP_{L,\mathrm{cwd}}}{dt} = \tau_{P,\mathrm{wood}}P_{P,\mathrm{wood}} - m_n\tau_{L,\mathrm{cwd}}P_{L,\mathrm{cwd}} \tag{D4}$$

$$\frac{dP_{S,\mathrm{mic}}}{dt} = \sum_j c_{\mathrm{mic},j}m_n\tau_{L,j}P_{L,j} + \sum_{kk} d_{\mathrm{mic},kk}\tau_{S,kk}P_{S,kk} - \tau_{S,\mathrm{mic}}P_{S,\mathrm{mic}},\ k \neq kk \tag{D5}$$

$$\frac{dP_{S,\mathrm{slow}}}{dt} = \sum_j c_{\mathrm{slow},j}m_n\tau_{L,j}P_{L,j} + \sum_{kk} d_{\mathrm{slow},kk}\tau_{S,kk}P_{S,kk} - \tau_{S,\mathrm{slow}}P_{S,\mathrm{slow}} - F_{P,\mathrm{tase}}\frac{\tau_{S,\mathrm{slow}}P_{S,\mathrm{slow}}}{\tau_{S,\mathrm{slow}}P_{S,\mathrm{slow}} + \tau_{S,\mathrm{pass}}P_{S,\mathrm{pass}}},\ k \neq kk \tag{D6}$$

$$\frac{dP_{S,pssss}}{dt} = \sum_j c_{\mathrm{pass},j}m_n\tau_{L,j}P_{L,j} + \sum_{kk} d_{\mathrm{pass},kk}\tau_{S,kk}P_{S,kk} - \tau_{S,\mathrm{pass}}P_{S,\mathrm{pass}} - F_{p,\mathrm{tase}}\frac{\tau_{S,\mathrm{pass}}P_{S,\mathrm{pass}}}{\tau_{S,\mathrm{slow}}P_{S,\mathrm{slow}} + \tau_{S,\mathrm{pass}}P_{S,\mathrm{pass}}},\quad k \neq kk \tag{D7}$$

$$\frac{dP_{S,\mathrm{lab}}}{dt} = \frac{F_{p,\mathrm{net}} + F_{p,\mathrm{dep}} + F_{p,\mathrm{fert}} + F_{p,\mathrm{wea}} + F_{P,\mathrm{tase}} - F_{p,\mathrm{up}} - F_{p,\mathrm{loss}} - \tau_{P,\mathrm{sorb}}\frac{S_{P\,\mathrm{max}}P_{S,\mathrm{lab}}}{K_{p\,\mathrm{lab}}+P_{S,\mathrm{lab}}}}{\left(1+\frac{S_{P\,\mathrm{max}}K_{p\,\mathrm{lab}}}{\left(P_{S,\mathrm{lab}}+K_{p\,\mathrm{lab}}\right)^2}\right)} \tag{D8}$$

$$\frac{dP_{S,\mathrm{sorb}}}{dt} = \frac{K_{p\,\mathrm{lab}}S_{p\,\mathrm{max}}}{\left(K_{p\,\mathrm{lab}}+P_{S,\mathrm{lab}}\right)^2}\frac{dP_{S,\mathrm{lab}}}{dt} \tag{D9}$$

$$\frac{dP_{S,\mathrm{ssb}}}{dt} = \tau_{P,\mathrm{sorb}}P_{P,\mathrm{sorb}} - \tau_{P,\mathrm{ssb}}P_{S,\mathrm{ssb}} \tag{D10}$$

Where $a_{P,i}$ is the allocation of P uptake to different plant pools, $F_{\mathrm{P,up}}$ is the plant P uptake ($\mathrm{g\,P\,m^{-2}\,d^{-1}}$), $r_{P,i}$ is the P resorption coefficient, $\tau_{P,\mathrm{sorb}}$ and $\tau_{P,\mathrm{ssb}}$ are rate constants for the sorbed and strongly sorbed P pools in $\mathrm{d^{-1}}$, respectively, both are equal to 0.01 $\mathrm{year^{-1}}$. $S_{p\,\max}$ and $K_{p\,\mathrm{lab}}$ are the maximum amount of sorbed P ($\mathrm{g\,P\,m^{-2}}$), and the constant for the adsorption ($\mathrm{g\,P\,m^{-2}}$), both parameters vary with soil order (see Table 2). $F_{p,\mathrm{net}}$, $F_{p,\mathrm{dep}}$, $F_{p,\mathrm{fert}}$, $F_{p,\mathrm{we}}$, $F_{p,\mathrm{up}}$ and $F_{p,\mathrm{loss}}$ are the net biological P mineralization, dust P deposition, fertilizer P addition, P weathering rate, plant P uptake rate and P loss rates, respectively; all are in $\mathrm{g\,P\,m^{-2}\,d^{-1}}$. $F_{p,\mathrm{tase}}$ is the biochemical P mineralization rate in $\mathrm{g\,P\,m^{-2}\,d^{-1}}$, and is calculated as

$$F_{p,\mathrm{tase}} = \frac{v_{p\,\max}\left(\lambda_{p\,\mathrm{up}} - \lambda_{p\,\mathrm{tase}}\right)}{\lambda_{p\,\mathrm{up}} - \lambda_{p\,\mathrm{tase}} + K_{p\,\mathrm{tase}}}\left(\tau_{S,\mathrm{slow}}P_{S,\mathrm{slow}} + \tau_{S,\mathrm{pass}}P_{S,\mathrm{pass}}\right) \tag{D11}$$

Where $v_{p\,\max}$ is the maximum specific biochemical P mineralization rate ($\mathrm{year^{-1}}$), $\lambda_{p\,\mathrm{up}}$ and $\lambda_{p\,\mathrm{tase}}$ are the N cost for P uptake and phosphtatse production ($\mathrm{g\,N\,(g\,P)^{-1}}$), respectively. $K_{p\,\mathrm{tase}}$ is an empirical constant. $\lambda_{p\,\mathrm{tase}}=15\,\mathrm{g\,N\,(g\,P)^{-1}}$ and $K_{p\,\mathrm{tase}}=150\,\mathrm{g\,N\,(g\,P)^{-1}}$ (see Wang et al., 2007). $\lambda_{p\,\mathrm{up}}$ and $v_{p\,\max}$ are biome-dependent model parameters.

Plant P uptake rate, $F_{p,\mathrm{up}}$, is calculated as

$$F_{p,\mathrm{up}} = \sum_i \left(a_{c,i}F_c\left(p_{P\,\max,i} - p_{P\,\min,i}\right) - r_{p,i}\tau_{P,i}P_{P,i}\right)\frac{P_{S,\mathrm{lab}}}{P_{S,\mathrm{lab}} + K_{\mathrm{P,up}}} + F_{p,\mathrm{up\,min}} \tag{D12}$$

where $p_{P\,\min,i}$ and $p_{P\,\max,i}$ are the minimal amd maximal P:C ratios of plant pool i, $K_{\mathrm{P,up}}$ is an empirical constant (=0.5 $\mathrm{g\,P\,m^{-2}}$). $F_{p,\mathrm{up\,min}}$ the minimal N uptake for a given NPP and is calculated as

$$F_{p,\mathrm{up\,min}} = \sum_i \left(a_{c,i}F_c p_{P\,\min,i} - r_{p,i}\tau_{P,i}P_{P,i}\right) \tag{D13}$$

Where $p_{P\,\min,i}$ and $p_{P\,\max,i}$ are minimal and maximal P:C ratios of leaf, wood or root in g P (g C)$^{-1}$, and varies with biome type, $K_{\mathrm{P,up}}$ is an empirical constant (=0.5 g P m^{-2}). Allocation of plant P uptake to leaf, wood and root is calculated similarly as plant N uptake.

Soil P can be lost by leaching. $F_{p,\mathrm{loss}}$ is calculated as

$$F_{p,\mathrm{loss}} = f_P P_{S,\mathrm{lab}} \tag{D14}$$

In this study we assumed that f_P=0.04 year^{-1} (see Hedin et al., 2003).

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Table 1. Biome specific model parameters. The IGBP biomes are evergreen needle leaf forest (1), evergreen broadleaf forest (2), deciduous needle leaf forest (3), deciduous broadleaf forest (4), mixed forest (5), shrub land (7), woody savannah (8), savannah (9), grassland (10), crop land (12), barren or sparse vegetation (16). We aggregate open and closed shrubland into shrubland and cropland mosaic into crop land. Wetland, urban land and land ice in the IGBP biome classification are not included in our simulations. The minimal N:C ratios and P:C ratios are 80% of their corresponding maximal values listed in this table for all plant tissue. The C:N and C:P ratios of the soil microbial biomass are 8 g C/g N and 32 g C/g P.

Parameter	Unit	1	2	3	4	5	7	8	9	10	12	16
a_{leaf}	Fraction	0.42	0.25	0.4	0.3	0.35	0.4	0.3	0.2	0.3	0.3	0.2
a_{wood}	Fraction	0.33	0.1	0.3	0.2	0.4	0.15	0.1	0.1	0	0	0.2
a_{root}	Fraction	0.25	0.65	0.3	0.5	0.25	0.45	0.6	0.7	0.7	0.7	0.6
$1/\tau_{\mathrm{P,leaf}}$	Year	2	1.5	0.8	0.8	1.2	1	1.5	1.5	1	1	1
$1/\tau_{\mathrm{wood}}$	Year	70	60	80	40	50	40	40	40	1	1	5
$1/\tau_{\mathrm{P,root}}$	Year	18	10	10	10	10	5	5	3	3	0.9	4
$1/n_{S,\mathrm{slow}}$	$\mathrm{g\,C/g\,N}$	16.1	12.8	24.8	30	10.1	19.3	15	15	13.1	13.2	26.8
$1/n_{S,\mathrm{pass}}$	$\mathrm{g\,C/g\,N}$	16.1	12.8	24.8	30	10.1	19.3	15	15	13.1	13.2	26.8
$1/n_{P\ \mathrm{max,leaf}}$	$\mathrm{g\,C/g\,N}$	50	25	60	50	50	40	25	25	50	25	40
$1/n_{P\ \mathrm{max,wood}}$	$\mathrm{g\,C/g\,N}$	250	150	250	175	175	150	150	150	150	125	150
$1/n_{P\ \mathrm{max,root}}$	$\mathrm{g\,C/g\,N}$	78	68	41	41	41	41	41	41	41	41	41
$1/p_{P\ \mathrm{max,leaf}}$	$\mathrm{g\,C/g\,P}$	400	375	480	500	500	320	375	375	650	250	400
$1/p_{P\ \mathrm{max,wood}}$	$\mathrm{g\,C/g\,P}$	3750	2250	3750	2625	2625	2250	2250	2250	2250	1875	2250
$1/p_{P\ \mathrm{max,root}}$	$\mathrm{g\,C/g\,P}$	1170	1020	615	615	615	615	615	615	615	615	615
$x_{np\ \mathrm{max}}$	–	1.51	1.28	1.59	1.42	1.42	1.36	1.30	1.26	1.46	1.21	1.37
$v_{p\ \mathrm{max}}$	–	1.6	1.0	1.6	1.6	0.6	0.8	1.6	1.6	0.8	0.8	1.6

Table 2. Soil order specific model parameters.

Number	Soil order	$K_{p\,\mathrm{lab}}$ g P m^{-2}	$S_{p\,\max}$ g P m^{-2}	P weathering rate g P m^{-2} year^{-1}	N:P newly formed SOM g N/g P
1	Alfisol	75	745	0.05	5
2	Andisol	68	788	0.04	5
3	Aridisol	78	1111	0.03	5
4	Entisol	64	745	0.02	5
5	Gellisol	64	745	0.01	5
6	Histosol	71	816	0.009	5
7	Inceptisol	65	747	0.008	5
8	Mollisol	54	722	0.007	5
9	Oxisol	10	293	0.006	7
10	Spodosol	28	311	0.005	7
11	Ultisol	64	373	0.004	7
12	Vertisol	32	616	0.003	7

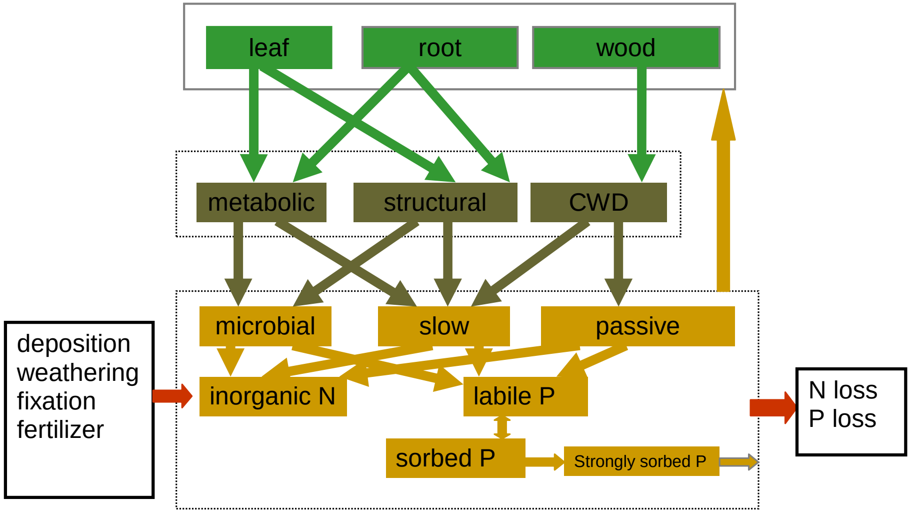

Fig. 1. Schematic representation of different pools and flows as represented in CASA-CNP model. Plant (green) is divided into leaf, root and wood, litter (dark brown) into metabolic litter, structural litter and coarse woody debris (CWD), soil (yellow brown) into microbial biomass, slow pool and passive pool. One inorganic soil mineral N pool and three other P pools are also represented. Arrows between the pools represent the direction of C, N and P flow between pools. For N and P, external inputs in red are deposition (N and P), weathering (P), fixation (N) and fertilizer addition (N and P), output in red is loss by leaching or gaseous loss from the ecosystem.

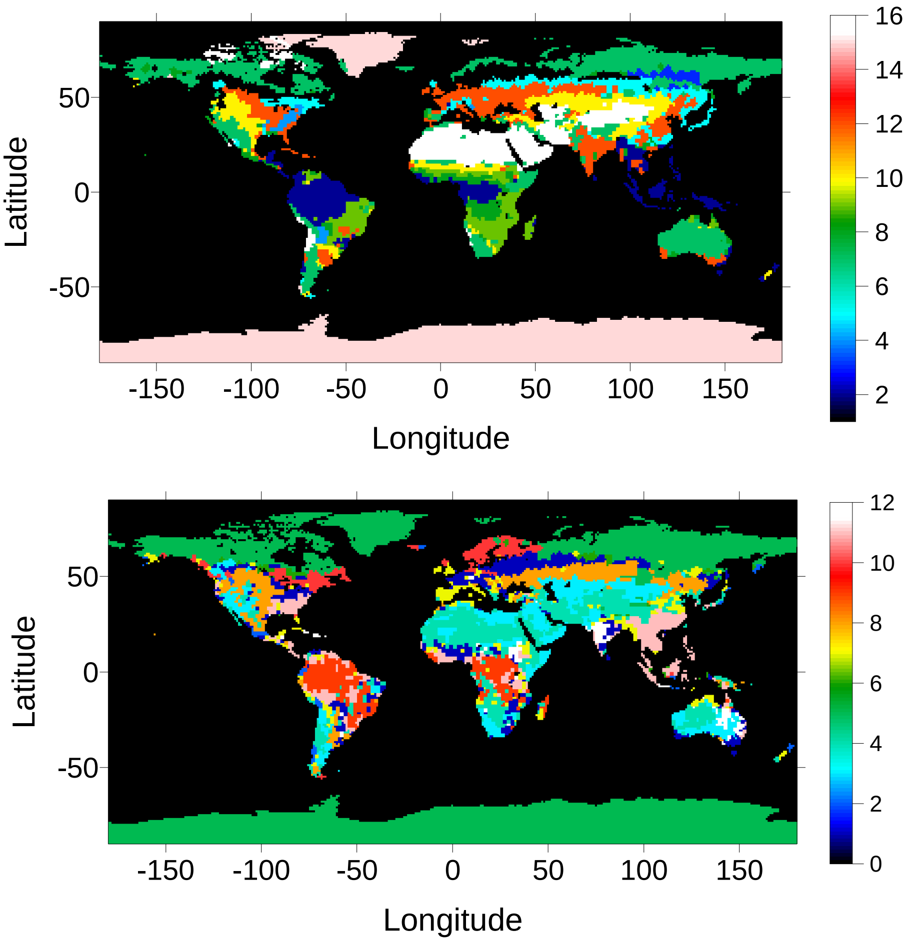

Fig. 2. IGBP vegetation map (upper panel, biome numbers are listed in Table 1) and USDA soil order map (lower panel, soil order numbers are listed in Table 2).

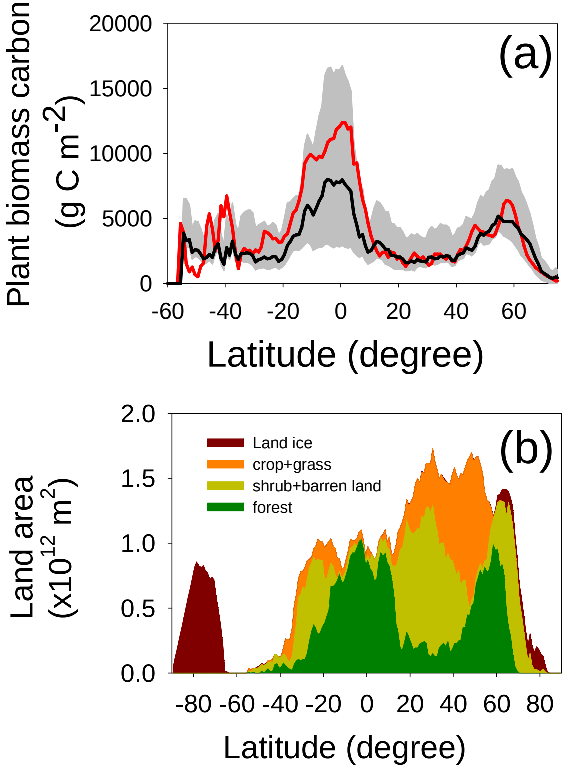

Fig. 3. **(a)** Comparison of the vegetation biomass carbon as estimated by CASACNP model (red) with those by Olsen et al. (1985) (black). The grey region represents the land area weighted mean of the maximal and minimal estimates of vegetation biomass carbon, and the black curve represents the land area weighted mean of the medium vegetation biomass carbon at different latitudes as estimated by Olsen et al. (1985); **(b)** the areas of forests, shrub land, crop land and grassland, and land ice at different latitudes.

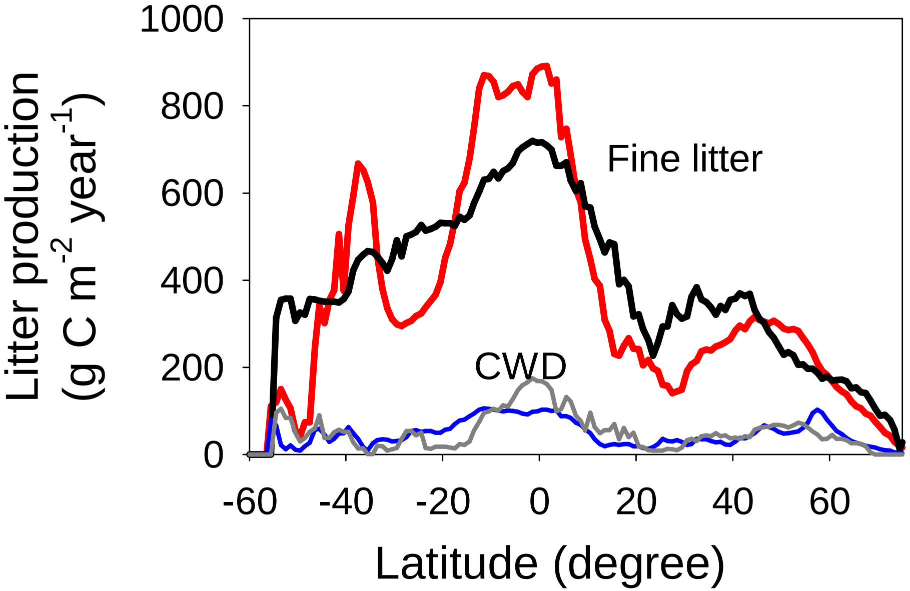

Fig. 4. Zonal mean for land grid points of fine litter production (red) and coarse woody litter production (blue) estimated by CASACNP as compared with those by Matthews (1997) (black for fine litter and grey for coarse woody debris).

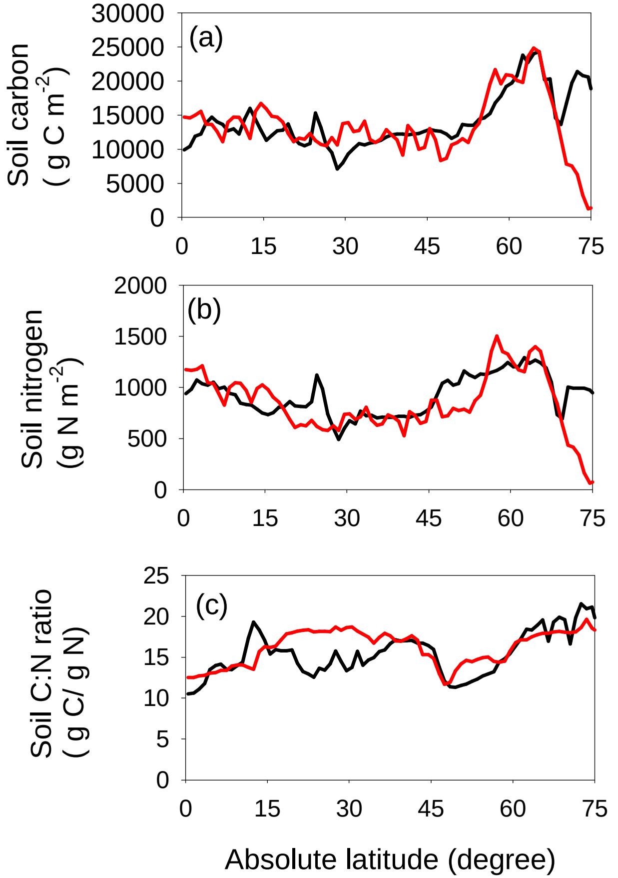

Fig. 5. Zonal mean of all land points of total C **(a)**, N **(b)** and C:N ratio **(c)** of soil organic matter by CASACNP (red) and Post et al. (1982, 1985) (black).

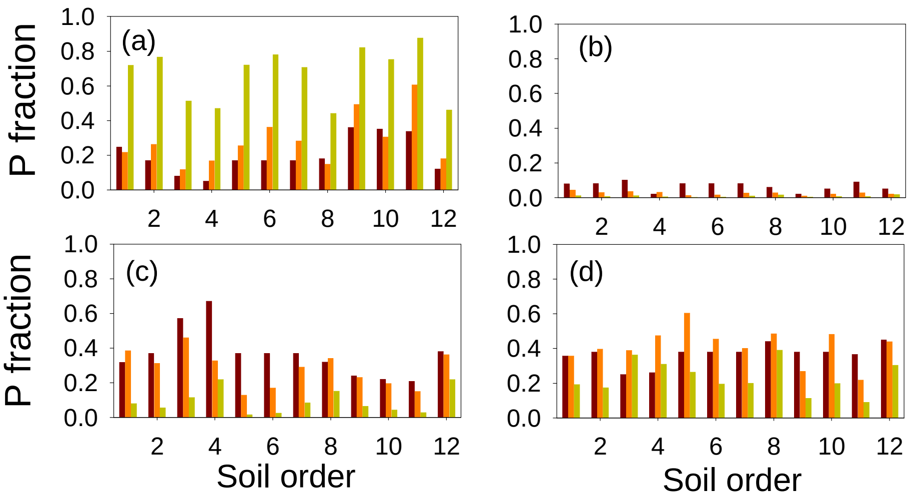

Fig. 6. Fraction of organic P **(a)**, labile P **(b)**, sorbed P **(c)** and strongly sorbed P **(d)** for each soil order for the top 15 cm soil field measurements from Cross and Schlesinger (1995) (dark red) as compared with the estimates by CASACNP with phosphatase production (orange) or without biochemical P mineralization (dark green). The soil orders from 1 to 12 are: alfisol, andisol, aridisol, entisol, gellisol, histosol, inceptisol, mollisol, oxisol, spodosol, ultisol and vertisol.

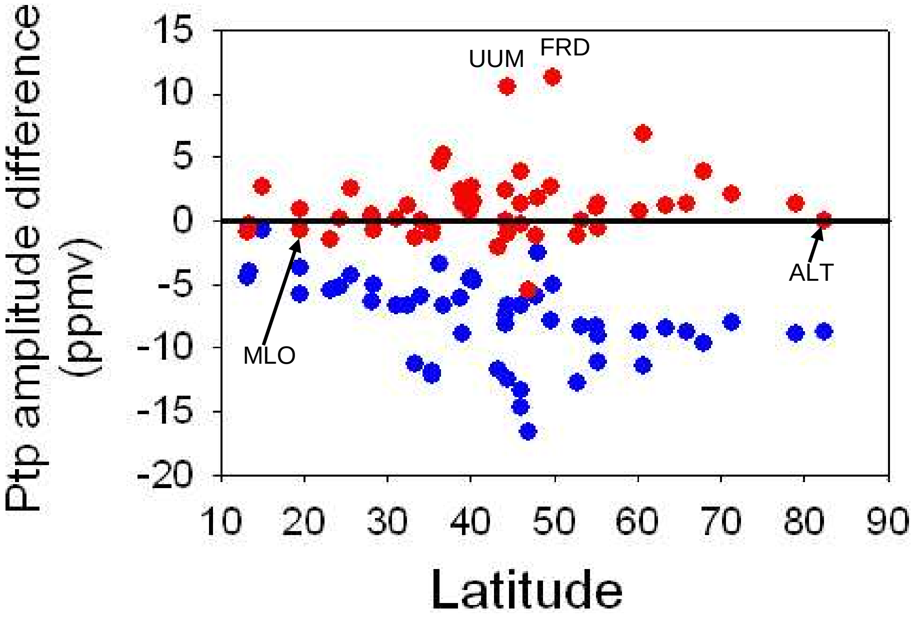

Fig. 7. Difference between simulated and observed peak-to-peak (ptp) amplitude of the seasonal cycle of atmospheric CO_2 for northern hemisphere observing sites (plotted by latitude). The observed ptp seasonal amplitudes are taken from the seasonal cycles provided in GLOBALVIEW-CO2 (2007). The simulated ptp seasonal amplitudes are reconstructed using response functions and monthly CASACNP carbon fluxes using a Q10 temperature dependence for litter and soil decomposition (red dots) or the Kirschbaum (1995) temperature dependence (blue dots). Four sites are labelled: Alert, Canada (ALT), Fraserdale, Canada (FRD), Ulaan Uul, Mongolia (UUM) and Mauna Loa, Hawaii (MLO).

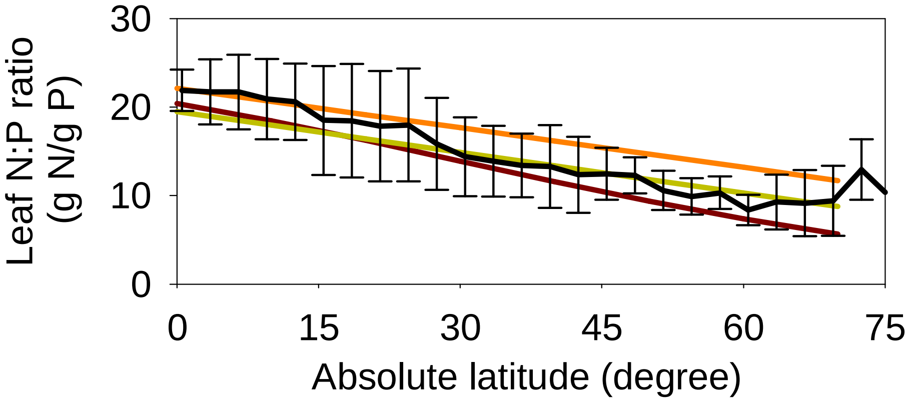

Fig. 8. Comparison of leaf N:P (g N/g P) as estimated by CASACNP (black curve) with the empirical relationships derived from different sets of field measurements by Reich and Oleksyn (2004) (dark brown), Kerkhoff et al. (2005) (orange) and Hedin (2004) (yellow green). The error bars represents the one standard error of the mean leaf N:P estimate by CASACNP within each latitudinal band.

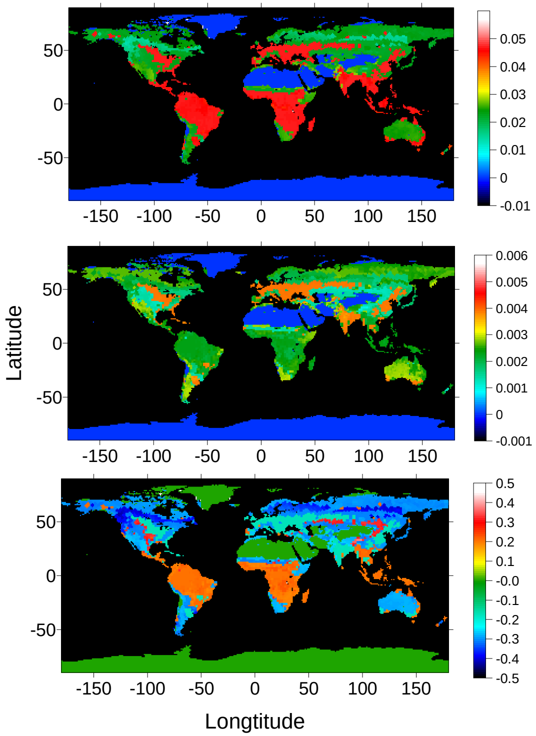

Fig. 9. Spatial variation of leaf N:C ratio (g N/g C) (the top panel), leaf P:C ratio (g P/g C) (middle panel) and the nutrient limitation factor on NPP (lower panel). The land type of permanent snow and ice are not modeled, and the values are set to zero. In order to show both N and P limitation variation spatially in the lower panel, we plotted the value of $x_{np}-1$ if $x_n<x_p$, or $1-x_{np}$ if $x_n>x_p$, where x_n is the N limiting factor on NPP, and x_p is the P limiting factor on NPP, $x_{np}=\min(x_n, x_p)$. Therefore regions with a negative value are limited by N and regions with a positive value are limited by P. A value of -0.2 corresponds to $x_{np}=x_n=0.8$, therefore addition of N fertilizer can increase NPP by 20%, similar for a P-limited region with a value of 0.2.

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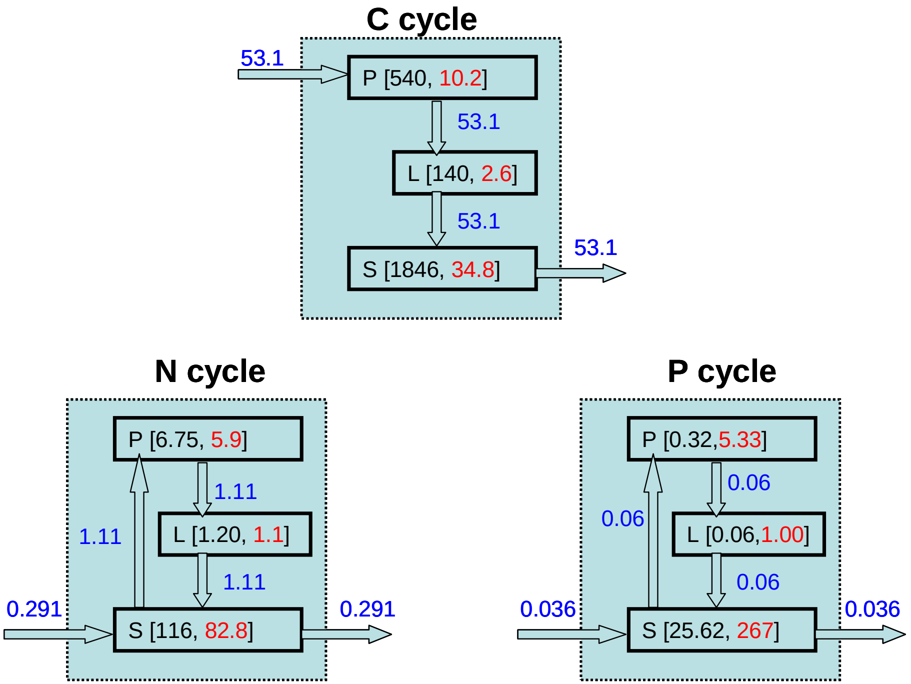

Fig. 10. Fluxes (blue), mean residence time (red) and pool sizes (black) of the C, N and P cycles in the terrestrial biosphere at steady state under present climate conditions. The external fluxes into the terrestrial biosphere or influx are indicated on the left-hand side and the fluxes out of the terrestrial biosphere or efflux are indicated on the right-hand side. The dotted squares represent the global terrestrial biosphere with three major compartments, plant (P), litter (L) and soil (S). The units of pool size are Gt C, N or P, the mean residence time is in years and the flux units are Gt C, N or P per year.