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Short Communication

Reconstruction of interannual variability of NEP using a process-based model (InTEC) with climate and atmospheric records at Fluxnet-Canada forest sites

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ABSTRACT: Reconstruction of interannual variability of net ecosystem productivity (NEP) in forests provides an important approach to analyse impacts of future climate change on global carbon (C) cycling. However, lacking climate data at sufficient temporal scales constrains NEP simulation and the potential of monthly climate data in modelling annual NEP remains largely poorly understood. In this study, annual NEP at 12 Fluxnet-Canada forest sites (93 site-year) was simulated using a process-based Integrated Terrestrial Ecosystem C-budget (InTEC) model driven by forest inventory data, site-level meteorological measurements, site-specific indicators, and remote sensing observations. Our results indicate that the InTEC model can capture the first order of interannual NEP variability with coefficients of determination (R^2) of 0.84 ($p < 0.001$) between simulated and measured NEP, providing a significant opportunity to reconstruct long-term climate change on forest C dynamics using only available monthly historical climate records. The usefulness of model simulation was further evaluated at three post-clearcut chronosequences Douglas-fir stands of British Columbia, suggesting that the Douglas-fir ecosystem would remain a C source for 15–20 years after clearcut and the maximum annual NEP may occur at the age around 50.

1. Introduction

Forest ecosystems play significant roles in global carbon (C) cycle (Pan *et al.*, 2011). Therefore, understanding of responses of forests to climate change will aid the policy decision in the context of future climate change, such as increasing droughts (Zhao and Running, 2010), rising CO_2 concentration (Norby *et al.*, 2010), and changes in precipitation (Knapp *et al.*, 2002). Net ecosystem productivity (NEP) is a key indicator of the C balance of an ecosystem, and represents the difference between gross primary production (GPP) and ecosystem respiration (R_e). It is, thus, a measure of the net exchange of C between the land surface and the atmosphere (Chen *et al.*, 2003; Grant *et al.*, 2010; Liu *et al.*, 2011; Wu *et al.*, 2012).

Reconstruction of impacts of historical climate on C uptake is particularly important as it provides a possible way to analyse responses of forests to climate change in future. The reliability of model simulation, however, is

difficult to assess and is commonly evaluated by comparing model simulations with short-term flux measurements and/or remote sensing observations (Xiao *et al.*, 2008; Grant *et al.*, 2010). These short-term measurements may serve as important landmarks to interpret model performance, and more importantly, they also suggest the idea of estimating NEP by appropriate combination of both historical climate records and recent benchmarking measurements. Such method would be a great advantage to model interannual NEP variability as short-term C cycle simulation would not be reliable for forests (Dunn *et al.*, 2007). A typical limitation in the reconstruction of annual NEP, however, is the unavailability of historical climate data with sufficient temporal resolution, which restricts the use of existing models running at either hourly (Grant *et al.*, 2010) or daily time step (Xiao *et al.*, 2008).

Although there are models using monthly climate data to estimate net primary productivity (NPP), the uncertainty in these input data should be reduced for improving our understanding of the regional impacts of global change (Pan *et al.*, 1996). This suggestion, however, imposes an underlying question on the potential of monthly climate data in capturing interannual C dynamics. For this purpose, we present an evaluation

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of reconstructing interannual variability of forest NEP using a process-based Integrated Terrestrial Ecosystem C-budget (InTEC) model with monthly climate data and atmospheric records as main inputs (Chen *et al.*, 2000a, 2000b). The usefulness of model outputs was further demonstrated by comparing simulated NEP with flux measurements at multiple sites representing a wide range of boreal and temperate forests in Canada.

2. Materials and methods

2.1. Study sites

By knowing a single study site and vegetation type, we cannot make full evaluation of the model performance. We therefore searched Fluxnet-Canada for selecting suitable sites (specific rules included the relatively long time of observations, good quality of flux and meteorological data, wide range of stand ages, etc.) and then 12 forest sites across Canada were selected with stand age ranging from 8 to 160 years. These sites cover varieties of forests with wide ranges of annual mean temperature ($0.2-8.5\,^{\circ}$C), mean precipitation ($467-1380\,$mm year^{-1}) and mean NEP (-600 to $600\,$g C m^{-2} year^{-1}). More detailed descriptions of these sites are provided in Table 1.

2.2. Flux data acquisition

Flux data provide continuous net ecosystem exchange (NEE) measurements and helps in mechanistic understanding of temporal and spatial variations of C fluxes. Half-hourly ecosystem CO_2 flux data were continuously measured at each site with the eddy-covariance technique (Baldocchi, 2003) and these data were obtained from Fluxnet-Canada archives (http://www.fluxnet-canada.ca).

Several procedures were applied to partition NEE (i.e. NEP) into GPP and R_e to facilitate the evaluation of model performances. The estimation of GPP and R_e was achieved by empirical relationships: (1) between night-time NEE and nighttime temperature, and (2) between daytime GPP and PAR. The procedures for gap-filling were those described by Barr *et al.* (2004) which was the standard method for all Fluxnet-Canada sites. First, the NEE is estimated as the sum of the measured eddy and air-column storage fluxes with two adjustments: (1) removal of low turbulence data, where a threshold value of friction velocity (u_*) is used to filter unacceptable fluxes (typically the threshold value was $0.35\,$m s^{-1} but differed slightly for some sites), and (2) an adjustment for poor energy-balance-closure, where turbulent fluxes (including NEE) are adjusted so that the sum of sensible and latent heat fluxes balances the net radiation minus the energy storage terms. Next, measured R_e is estimated as $R_e = -$NEP during periods when GPP is zero, i.e. at night and during both night and day in the cold season [periods when both air (T_a) and 2 cm soil (T_s) temperatures are less than $0\,^{\circ}$C]. Finally, GPP is estimated as NEP $+ R_e$ (daytime) or set to zero (nighttime and during periods when both T_a and T_s are less than $0\,^{\circ}$C).

2.3. Model simulation strategy

2.3.1. Model overview

The InTEC model is a process-based biogeochemical C-budget model and considers all major C cycle components (Chen *et al.*, 2000a, 2000b). This model adopts a distinct approach to simulate C components by combining (a) Farquhar's leaf-level biochemical model (Farquhar *et al.*, 1980), (b) a soil biochemical model

Table 1. Description of the study sites.

| Sites	Latitude	Longitude	Data range	Descriptions	References
CA-OAS	53.6288	−106.1977	1997−2008	Mature aspen with a few balsam poplar, thick hazel understory	Barr *et al.* (2004)
CA-OBS	53.9871	−105.1177	1999−2008	Mature black spruce overstory, feather moss ground cover	Barr *et al.* (2004)
CA-OJP	53.9163	−104.6920	2000−2007	Mature jack pine overstory, very sparse green alder understory, predominantly lichen ground cover	Coursolle *et al.* (2006)
CA-QCU	49.2671	−74.0365	2003−2008	Regenerating black spruce, Vaccinium spp., Ledum, moss	Giasson *et al.* (2006)
CA-MAN	55.8800	−98.4810	1995−2008	Black spruce, occasional larch present in poorly drained areas	Dunn *et al.* (2007)
CA-CA1	49.8672	−125.3336	1999−2008	Old Douglas-fir with 17% red cedar and 3% western hemlock	Jassal *et al.* (2009)
CA-CA2	49.8705	−125.2909	2001−2008	Douglas-fir, grasses, woody shrubs, bracken fern	Jassal *et al.* (2009)
CA-CA3	49.53462	−124.9004	2002−2008	Old Douglas-fir, understory consisting of fireweed, salal, Oregon grape	Jassal *et al.* (2009)
CA-SJ1	53.9084	−104.6559	2002−2005	Jack pine, grass and shrub ground cover	Barr *et al.* (2004)
CA-SJ2	53.9447	−104.6559	2003−2008	Jack pine seedlings, grasses, herbs, lichen, dead wood	Barr *et al.* (2004)
CA-SJ3	53.8758	−104.6453	2004−2007	Jack pine overstory, with alder and lichen ground cover	Barr *et al.* (2004)
CA-QFO	49.6925	−74.3420	2005−2008	Black spruce with a few jack pine and tamarack	Margolis *et al.* (2006)
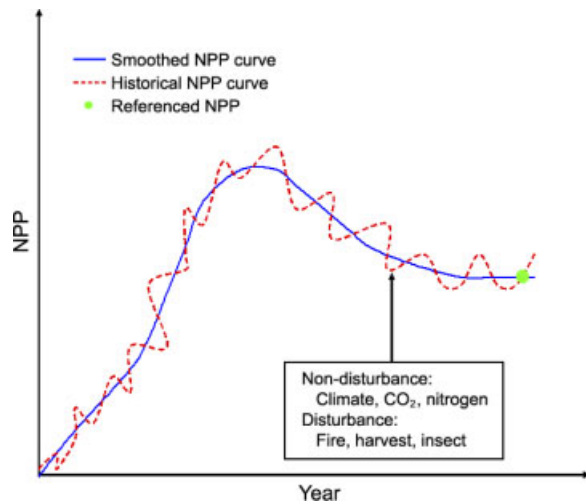
Figure 1. A description of the core components of the InTEC model.

CENTURY (Parton *et al.*, 1994) modified to include forest-specific C pools such as coarse roots and woody detritus, and (c) a set of empirical NPP and age relationships derived from forest growth and yield data (Chen *et al.*, 2002; He *et al.*, 2012).

The empirical NPP–age relationship is normalized between 0 and 1 and the shape of the curve (e.g. maximum occurrence) is empirically determined as a function of the mean annual air temperature (Chen *et al.*, 2003). Approaches to simulate major C fluxes, i.e. GPP, autotrophic respiration (R_a) and heterotrophic respiration (R_h), as well as influences of disturbances are provided in the Appendix. Figure 1 illustrates the two core components of the InTEC model: (1) the age-dependent productivity of forests, and (2) the combined effects on NPP of both disturbances (fire, harvest, and insect) and nondisturbances (climate, CO_2, and nitrogen). The InTEC model adopts this unique way of combining recent remote sensing information with historical climate data for long-term forest C dynamics simulation.

The smoother NPP curve in Figure 1 is achieved by iteratively calculating NPP using the above procedures until the annual NPP value in a reference year (e.g. 2006 in this study) simulated by InTEC equals to the prior known value. This step reconstructs a smoothed variation of NPP using the stand age of the site and an empirical NPP–age relationship as below.

$$\mathrm{NPP}\,(\mathrm{age}) = a \left(\frac{1 + b \left(\frac{\mathrm{age}}{c} \right)^d - 1}{\exp \left(\frac{\mathrm{age}}{c} \right)} \right) \quad (1)$$

where a, b, c, and d are coefficients and can be determined from the mean annual temperature (T_a) as provided in Chen *et al.* (2002).

The second step is considered as producing the interannual variability of NPP in which both impacts of disturbances and nondisturbances are superimposed on the

smooth NPP curve to predict the historical NPP curve by

$$\mathrm{NPP}\,(i) = \mathrm{NPP_u}\,(i)\,\mathrm{Fnpp}\,(i) \quad (2)$$

where $\mathrm{NPP_u}(i)$ is NPP value determined by nondisturbance factors in year i, $\mathrm{Fnpp}(i)$ is the i year normalized forest productivity changing with age (0–1).

The InTEC model aims to simulate long-term (from 1901 to 2006) C cycling but it does not calculate the absolute values of NPP in each year (Ju *et al.*, 2007). Instead, the model reconstructs the interannual variability in NPP through the following equations:

$$\mathrm{NPP_u}\,(i) = \mathrm{GPP}(i) - R_a(i)$$

$$\mathrm{NPP_u}\,(i-1) = \mathrm{GPP}(i-1) - R_a(i-1)$$

$$\frac{\mathrm{NPP_u}\,(i) - \mathrm{NPP_u}\,(i-1)}{\mathrm{NPP_u}\,(i) + \mathrm{NPP_u}\,(i-1)}$$

$$= \frac{\mathrm{GPP}\,(i) - \mathrm{GPP}\,(i-1) - R_a\,(i) + R_a\,(i-1)}{\mathrm{GPP}\,(i) + \mathrm{GPP}\,(i-1) - R_a\,(i) - R_a\,(i-1)}$$

$$= \frac{(X\,(i) - 1) - \beta\,(i-1)\,(Y\,(i) - 1)}{(X\,(i) + 1) - \beta\,(i-1)\,(Y\,(i) + 1)} = B\,(i) \quad (3)$$

Therefore,

$$\mathrm{NPP_u}\,(i) = \mathrm{NPP_u}\,(i-1)\,\frac{1 + B\,(i)}{1 + B\,(i)} \quad (4)$$

where $X(i)$ is the interannual variability of GPP between year i and year $i-1$, which is calculated using modified InTEC model's approach, $\beta(i-1)$ is the ratio of autotrophic respiration to GPP in year $i-1$, and $Y(i)$ is the interannual variability of autotrophic respiration in year i and year $i-1$. After the long-term simulation, InTEC model then compares the simulated NPP in the reference year with the benchmark NPP to evaluate if recalculation is needed (e.g. the difference between InTEC simulates and benchmark NPP should be within 5%).

2.3.2. *Model dataset*

The dataset used to simulate NEP for all sites include (1) a forest stand age map developed using gridded forest inventory (He *et al.*, 2012), (2) gridded monthly climate data (temperature, precipitation) since 1901 (Gullett and Skinner, 1992), (3) soil texture data from the Soil Landscapes of Canada (Lacelle, 1998), (4) nitrogen deposition interpolated from the Canadian Air and Precipitation Monitoring Network (Chen *et al.*, 2000a, 2000b) and CO_2 concentration acquired from Keeling and Whorf (1996), and (5) site-level leaf area index (LAI) (Gonsamo and Chen, 2011). In particular, for years that flux data are observed, which are indicated by the data time range in Table 1, all those input variables will be replaced by tower-based measurements, including flux (e.g. referenced NPP), meteorological observations (e.g. temperature, precipitation, etc.) and site index (e.g. age, LAI, etc.).

To constrain the simulation, InTEC model needs a reference NPP in a recent year (e.g. 2006 in this study),
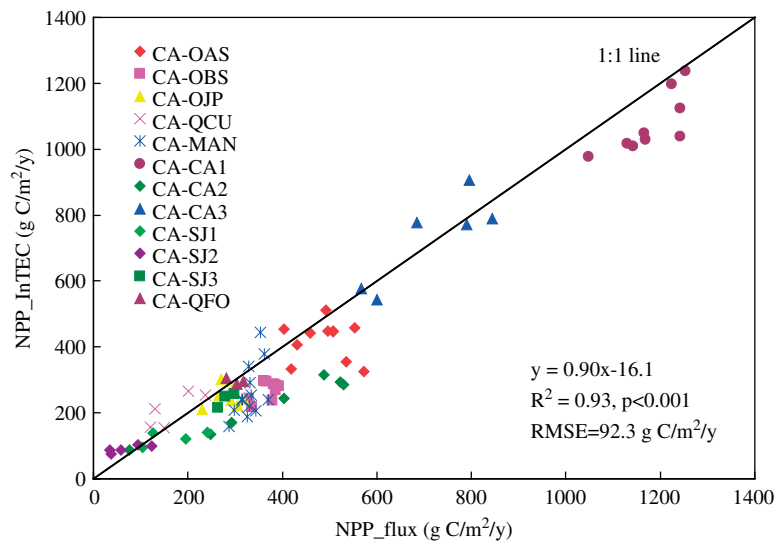
Figure 2. Relationship between flux-measured net primary productivity (NPP, NPP_flux) and InTEC-modelled NPP (NPP_InTEC) for all sites.

which was obtained from the boreal ecosystem productivity simulator (BEPS) previously (Liu *et al.*, 2002). To exclude uncertainties from using model-simulated NPP, we used flux-measured GPP with an additional empirical determination of R_a (i.e. assuming NPP is 47% of annual GPP) (Waring and Running, 1998). A similar approach was reported for Canadian forest ecosystems (Grant *et al.*, 2010), which confirms the use of this empirical method in our study. Owing to limited flux data at CA-SJ1 (from 2002 to 2005), only in this site the BEPS-simulated NPP was assigned for 2006 to proceed the modelling. To reduce autocorrelation in the validation of InTEC, both NPP and NEP for the referenced years were excluded because these NPP values were used to constrain simulation. Therefore, the overall data for the later model validation are 82 site-year.

3. Results and discussion

We obtained promising results with site-level InTEC model. As shown in Figure 2, coefficients of determination (R^2) equalled to 0.93 ($p < 0.001$) was observed between the flux-measured NPP and InTEC-modelled NPP and the corresponding root mean square error (RMSE) was 92.3 g C m^{-2} year^{-1} for the overall dataset. This result indicates that the InTEC model can provide a reliable approach to link historical data with recent flux observations in reconstructing NPP curves across forests from diverse ecoregions of various ages.

With a strategy of modelling R_h by nine biomass pools to simulate soil C dynamics, R^2 of 0.84 ($n = 82$, $p < 0.001$) was obtained when the InTEC-modelled NEP were compared with the flux measurements (Figure 3). The RMSE of modelled NEP was about 84.2 g C m^{-2} year^{-1}, which was roughly 7% of the

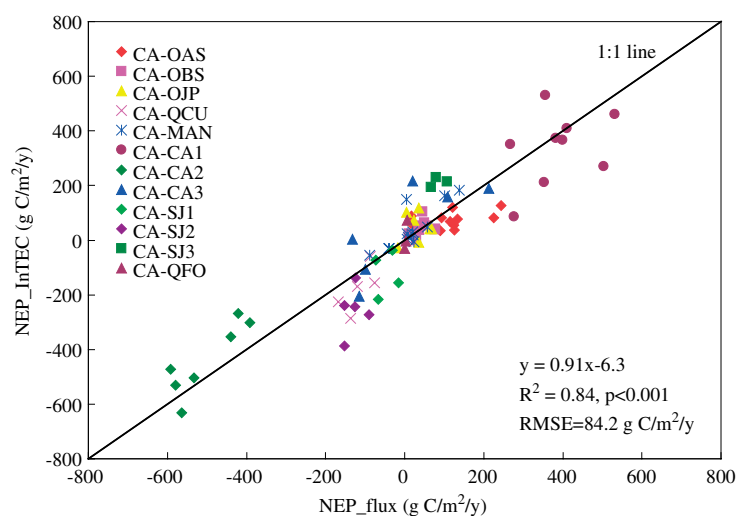Figure 3. Relationship between flux-measured net ecosystem productivity (NEP, NEP_flux) and InTEC-modelled NEP (NEP_InTEC) for all sites.
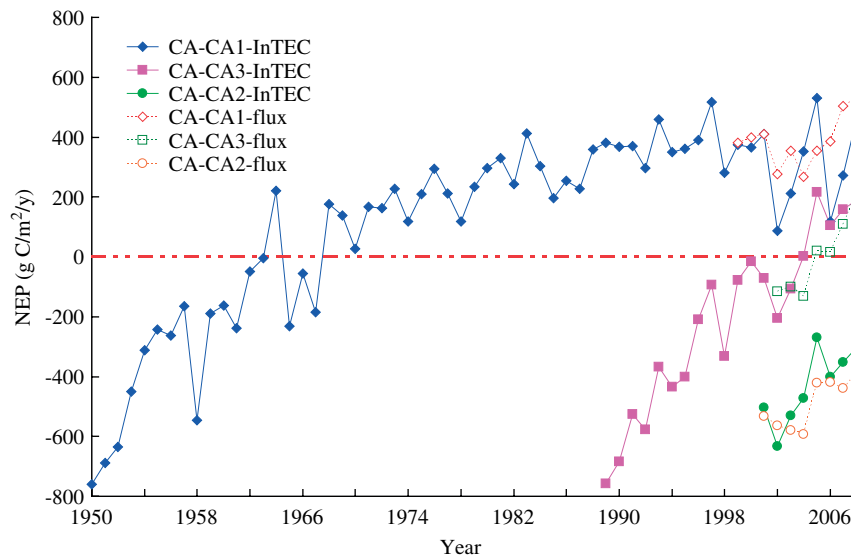
Figure 4. Descriptions of chronosequence NEP for the three different-aged Douglas-fir stands. The red dash line indicates the difference between carbon sink and source.

dynamic ranges of all NEP observed. When comparing data of single site, this correlation differs substantially with R^2 ranges from 0.18 ($p = 0.228$) for CA-CA1 to the highest of 0.72 ($p < 0.001$) for site CA-MAN. We suggest that it is reasonable given the short period of flux observations and limited sample years for most of these sites.

The most advantage of running InTEC model at flux towers is the reduced uncertainties for input variables, such as the climate parameters and site-specific indicators. This is important to show the potential of InTEC model in simulating C dynamics. As suggested by Chen *et al.* (2003), the referenced NPP is considered to have the largest impact on the modelled NEP with an uncertainty of approximately 30%. Instead of using model-simulated NPP in previous versions, which roughly has an error of 25%, we used the flux-derived NPP for all sites to constrain the simulation process. This site-level validation shows that InTEC model can provide a reliable approach to simulate C dynamics using site-level inputs and flux observations. In particular, the results indicate that simulation of NEP at monthly time steps can capture its first order of interannual variability, as historical climate data (last 100 years) are only available at monthly time step. Compared to the results obtained at the regional scale in previous work (Chen *et al.*, 2003), our analysis is the first validation of the InTEC model showing its power in predicting ecosystem C uptakes with flux measurements and recent remote sensing data. This would be a necessary step and premise for the future investigation of regional C dynamics with InTEC model.

We also analysed the impact of forest harvest on ecosystem NEP with data at CA-CA1, CA-CA3, and CA-CA2 of the same Douglas-fir forest, which were harvested in 1949, 1988, and 2000, respectively. This is also a practical use of the InTEC model for modelling C uptake over long-time scales. Historical variations in annual NEP were reconstructed using InTEC model with

monthly climate data and the referenced NPP in 2006 (Figure 4). The simulation indicates that after the initial removal of forests, the ecosystem became a large C source with an annual NEP around $-800 \, \text{g C m}^{-2} \, \text{year}^{-1}$ and then gradually moved towards C sink. The time duration of net C source may differ substantially across regions, depending on the variations and amplitudes of R_h. When comparing three sites of Douglas-fir stands, we suggest that the ecosystem will remain a C source for the following 15–20 years after harvest. However, this duration could be shortened with both increase of temperature and CO_2 concentration in recent years, which is shown at CA-CA3. The ecosystem then acts as a C sink and annual NEP would increase for approximately 30 years before reaching the maximum value.

The most distinct feature of the InTEC model compared with other coupled C-climate models is its incorporation of the NPP–age relationship of forests, by which InTEC considers the structural changes associated with stand development through time. This is important as increasing evidences are shown that stand age plays an important role in forest growth and neglecting the age effect may lead to incorrect responses of NPP to other factors (He *et al.*, 2012). A typical uncertainty of the InTEC model is the underestimation of both NPP and NEP, as most of the scatter points in Figures 2 and 3 are below the 1:1 line. These underestimations have been previously given by Chen *et al.* (2003) and (Ju *et al.*, 2007). While this observation for the three Douglas-fir stands may be caused by the extra fertilization of stand treatments (Grant *et al.*, 2010), a more deep analysis should be focussed on issues such as C/N ration and soil respiration (Luo *et al.*, 2001), which requires further investigations of proper parameterization of model inputs. We suggest that the determination of Q_{10} (2.3 for all biomass) probably needs further considerations. This could be the reason for the overestimation of autotrophic

respiration of the InTEC model and thus underestimates both NPP and NEP.

The other uncertainty is associated with the model approach that the accumulated sensitivity from monthly observed temperatures within a year may not reflect the C cycle probably, which may be the reason for the inappropriate predictions of NEP for all three Douglas-fir stands in 2004, a year with a particularly warm summer. This imposes questions of model performance under severe droughts and heat waves. Although the results of NEP are presented here, the core part of InTEC is the reconstruction of NPP curve. Instead of calculating the absolute values of NPP data in a specific year, InTEC model uses the interannual variability in annual NPP derived from climate records and the NPP–age relationship. Uncertainties exist when the NPP–age relationship derived from limited sites is applied for diverse ecosystems located at various ecoregions. Therefore, care should be given with respect to parameterization of the empirical NPP–age relationship.

4. Conclusions

With monthly historical climate data and recent flux observations, long-term responses of forest NEP to climate change were reconstructed using a process-based InTEC model. The validation using flux data from 12 sites at various ecoregions across Canada indicates that the InTEC model can provide reasonable well NEP estimates with a R^2 value of 0.84 ($p < 0.001$) for the overall 81 year-site data. This stand level evaluation supports the use of monthly historical climate data in capturing interannual variability of NEP. Although with shortcomings in characterizing input variables, the InTEC model adopts a unique way to link historical climate data with recent benchmark observations, which provides meaningful insights for the understanding of future climate change on the global C cycle.

Acknowledgements

Appendix

The GPP is scaled up using Farquhar's biochemical model from leaf to canopy,

$$\text{GPP} = \int_t P_{\text{can}}(t)\,dt$$

$$P_{\text{can}} = P_{\text{can1}}f_p + P_{\text{can2}}\left(1 - f_p\right)$$

$$P_{\text{can1}} = (J_{\text{sun}}L_{\text{sun}} + J_{\text{shade}}L_{\text{shade}})\,\frac{C_i - \Gamma}{4.5C_i + 10.5\Gamma},$$

$$P_{\text{can2}} = V_{\text{m}}\frac{C_i - \Gamma}{C_i + k}L_t, \quad L_{\text{sun}} = 2(1 - p\,(\theta))\cos\theta,$$

$$L_{\text{shade}} = L_t - L_{\text{sun}} \tag{A1}$$

where P_{can1} and P_{can2} are canopy gross photosynthesis limited by electron transport and rubisco activity, respectively, and f_p is the fraction of canopy photosynthesis limited by P_{can1}. L_t, L_{sun}, and L_{shade} are the total, sunlit, and shaded LAI, respectively. $p(\theta)$ is the gap fraction at the view Zenith angle θ, given by $p(\theta) = \exp(-G(\theta)\Omega L_t/\cos\theta)$ (Chen and Leblanc, 1997). J, V_{m}, C_i, Γ, and k are calculated from air temperature, radiation, and CO_2 concentrations as in Bonan (1995),

$$J = \left[J_{\text{m}} + 0.38S - \sqrt{(J_{\text{m}} + 0.38S)^2 - 1.064J_{\text{m}}S}\right]/1.4,$$

$$J_{\text{m}} = J_{\text{m25}}\frac{N_1}{N_{1\,\text{max}}}a_{\text{jm}}^{(T_a-25)/10}/\left[1 + e^{(85.4T_a - 3147.7)/(T_a+273)}\right]$$

$$= J_{\text{m25}}\frac{N_1}{N_{1\,\text{max}}}J_{\text{mt}},$$

$$V_{\text{m}} = V_{\text{m25}}\frac{N_1}{N_{1\,\text{max}}}a_{\text{vm}}^{(T_a-25)/10}/\left[1 + e^{(85.4T_a - 3147.7)/(T_a+273)}\right]$$

$$= V_{\text{m25}}\frac{N_1}{N_{1\,\text{max}}}V_{\text{mt}},$$

$$\Gamma = 40.2 \times 1.75^{(T_a-25)/10},$$

$$k_{\text{co}} = 300 \times 2.1^{(T_a-25)/10} + 209 \times 1.75^{(T_a-25)/10},$$

$$C_i = \alpha C_a$$

where T_a is air temperature, S (W m^2) is incoming solar radiation, N_1 (g N m^{-2}) and $N_{1\text{max}}$ (g N m^{-2}) are actual and maximum leaf N content, V_{m25} (μmol CO_2 m^{-2} s^{-1}) and J_{m25} (μmol CO_2 m^{-2} s^{-1}) are carboxylation and electron transport rates at 25 °C, a is the ratio of intercellular CO_2 concentration to the atmospheric CO_2 concentration, determined by soil water availability, a_{jm} and a_{vm} are sensitivity of electron transport and rubisco activity to temperature, with values of 1.75 and 2.4, respectively, and C_a is atmospheric CO_2 concentration (ppmv).

R_a is determined through biomass pools of several components,

$$R_{\text{a}} = \left(C_l R_{l,15} + C_{\text{w}} R_{\text{w},15} + C_{\text{cr}} R_{\text{cr},15} + C_{\text{fr}} R_{\text{fr},15}\right)$$
$$\times Q_{10}^{(T-15)/10} \tag{A2}$$

where C_l, C_s, C_{cr}, and C_{fr} are respiratory C in foliage, woody, coarse root, and fine root biomass pools, $R_{l,15}$, $R_{\text{s},15}$, $R_{\text{cr},15}$, and $R_{\text{fr},15}$ are annual respiration rates at an annual mean temperature of 15 °C, T is annual mean temperature, and Q_{10} is the temperature sensitivity of maintenance respiration to temperature, being 2.3 used for all biomass pools (Ju et al., 2007).

R_h is calculated using algorithms adopted from the CENTURY model using nine pools to simulate soil C dynamics,

$$R_h = \sum_{j=1}^{9} k_{j,a} C_j \tag{A3}$$

where $k_{j,a}$ (year^{-1}) is the rate of C released from the jth C pool, and C_j (g C m^{-2}) is the size of the jth C pool.

The decomposition rates of C pools are the products of maximum rates modified by soil temperature, moisture, texture, N availability, and lignin content (litter pools):

$$k_j(i) = \begin{cases} K_j KN_j(i) A(i) LC_j, j = 1, 2, 3 \\ K_j KN_j(i) A(i), j = 4, 5, 8, 9 \\ K_j A(i) T_m, j = 6 \\ K_j A(i), j = 7 \end{cases} \tag{A4}$$

where K_j (year^{-1}) is the maximum decomposition rate of the jth pool ($K_j = 3.9, 4.9, 2.4, 14.8, 18.5, 6.0, 7.3, 0.2, 0.0045$ year^{-1}), $KN_j(i)$ (dimensionless) is the modifier for the effect of N availability on C decomposition, $A(i)$ (dimensionless) is the combined abiotic effect of soil temperature and moisture on soil C decomposition, T_m (dimensionless) is the effect of soil texture on soil microbial turnover, and LC_j (dimensionless) is the impact of lignin content on structural litter decomposition.

Disturbances are important for direct C release and the direct emission of C to the atmosphere $R_d(i)$ in InTEC model is set to zero in nondisturbed years and estimated using a simplified model of Kasischke *et al.* (2000) in the disturbed year

$$R_{(d)}(i) = C_1(i) + 0.25 C_w(i) + C_{ssd}(i) + C_{smd}(i) \tag{A5}$$

where $C_1(i)$, $C_w(i)$, $C_{ssd}(i)$, and $C_{smd}(i)$ are sizes of foliage, woody, surface structural, and surface metabolic litter C pools (Ju *et al.*, 2007). Owing to the unavailability of accurate data for all the disturbances, InTEC model treats all disturbances as fire and assumes that a fire disturbance would release to the atmosphere 100% of the C contained in foliage, 25% of that in aboveground woody material and all fine fuel (foliage detritus) (Chen *et al.*, 2003).

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