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# Modeling carbon dynamics in two adjacent spruce forests with different soil conditions in Russia

J. Kurbatova<sup>1</sup>, C. Li<sup>2</sup>, A. Varlagin<sup>1</sup>, X. Xiao<sup>2</sup>, and N. Vygodskaya<sup>1</sup>

<sup>1</sup>A. N. Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Moscow, Russia

<sup>2</sup>Institute for the Study of Earth, Oceans, and Space, University of New Hampshire, Durham, NH03824, USA

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Correspondence to: C. Li (Changsheng.li@unh.edu)

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## Abstract

Net ecosystem carbon exchange (NEE) were measured with eddy covariance method for two adjacent forests located at the southern boundary of European taiga in Russia in 1999–2004. The two spruce forests shared similar vegetation composition but differed in soil conditions. The wet spruce forest (WSF) possessed a thick peat layer (60 cm) with a high water table seasonally close to or above the soil surface. The dry spruce forest (DSF) had a relatively thin organic layer (5 cm) with a deep water table (>60 cm). The measured NEE fluxes (2000 and  $-1440 \text{ kg C ha}^{-1} \text{ yr}^{-1}$  for WSF and DSF, respectively) indicated that WSF was a source while DSF a sink of atmospheric carbon dioxide during the experimental years. A process-based model, Forest-DNDC, was employed in the study to interpret the observations. The modeled NEE fluxes were 1800 and  $-2200 \text{ kg C ha}^{-1} \text{ yr}^{-1}$  for WSF and DSF, respectively, which were comparable with the observations. The modeled data indicated that WSF and DSF had similar rates of photosynthesis and plant autotrophic respiration but differed in soil heterotrophic respiration. The simulations resulted in a hypothesis that the water table fluctuation at WSF could play a key role in determining the negative C balance in the ecosystem. A sensitivity test was conducted by running Forest-DNDC with varied water table scenarios for WSF. The results proved that the NEE fluxes from WSF were highly sensitive to the water table depth. When the water table dropped, the length of flooding season became shorter and more organic matter in the soil profile suffered from rapid decomposition that converted the ecosystem into a source atmospheric C. The conclusion from this modeling study could be applicable for a wide range of wetland and forest ecosystems that have accumulated soil organic C while face hydrological changes under certain climatic or land-use change scenarios.

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## 1 Introduction

Boreal forests contain about 50% of the total carbon stored in vegetation and soils in the world (Dixon et al., 1994). The majority of boreal forests are distributed in Russia (600 million ha), Europe (300 million ha) and North America (500 million ha) (Schulze et al., 1999). Although relatively simple in their vegetation composition and structure, boreal forests play an important role in the global cycles of carbon (C), water and nutrients as well as the climate system. A number of global C balance studies have suggested that there is very likely a large C sink in the northern Hemisphere, but its spatial patterns and temporal dynamics remain uncertain (Schimel et al., 2001; Fan et al., 1998; Myneni et al., 2001). Multiple biological and abiotic factors, including climate variation, land use change, and frequent natural disturbance (e.g. fire, insect outbreak), could significantly affect the carbon dioxide (CO<sub>2</sub>) fluxes and C storage in the boreal forest regions (Shvidenko and Nilsson, 2002; Jarvis and Linder, 2000; Kobak et al., 1996). The existing estimates of net primary production for boreal forests vary widely (Melillo et al., 1993; Schulze et al., 1999; Jarvis et al., 2001; Jarvis and Linder, 2000).

To better quantify the role of boreal forests in the global carbon cycle, the international research communities recently made great efforts establishing a net work of CO<sub>2</sub> eddy flux towers across boreal forests in Northern Eurasia through programs as AsiaFlux, EuroFlux, and ChinaFlux (Schulze et al., 1999; Hollinger et al., 1998; Roeser et al., 2002; Lloyd et al., 2002; Hamada et al., 2004; Ohta et al., 2001). The eddy flux tower network has produced and will continuously produce rich data sets of net ecosystem exchange of CO<sub>2</sub> (NEE) between forests and the atmosphere at the tower sites. NEE is defined as the difference between gross primary production (GPP) and ecosystem respiration ( $R_e$ ) consisting of the plant autotrophic respiration and the soil microbial heterotrophic respiration. Preliminary analyses with the observed NEE flux data have been conducted and demonstrated interesting but complex patterns on the seasonal dynamics and inter-annual variations of the NEE fluxes (Falge et al., 2002).

Carbon dynamics represented by the observed NEE fluxes for the forest ecosystems

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is regulated by a series of primary drivers including climate, soil, hydrology, vegetation, and management practices. Any single change in the primary drivers could simultaneously alter several of the forest environmental factors such as radiation, temperature, soil moisture, soil redox potential, and nutrient substrates dynamics; and the altered environmental factors could collectively and simultaneously affect the plant photosynthesis and/or the ecosystem respiration (Li, 2007). Sometimes, the interactions between the changes in primary drivers and the forest responses are so complex that it is hard to reveal the mechanisms controlling the forest C dynamics solely relying on the observed NEE fluxes. Process-based models have been developed to meet the gap. During the past decade a number of models were developed by integrating the fundamental processes that governing forest growth, litter incorporation, and soil organic matter (SOM) turnover. Driven by climate, forest type, soil properties, management practices and other relevant input parameters, the models can simulate forest production as well as C and N cycles in the ecosystems. Among the modeling efforts, the Forest-DNDC model developed by Li and his colleagues (Li et al., 2000) has been tested for greenhouse gas studies with encouraging results (Stange et al., 2000; Butterbach-Bahl et al., 2004; Kiese et al., 2004; Cui et al., 2005; Kesik et al., 2005; Miehle et al., 2006) . In this study, we applied Forest-DNDC for understanding the NEE fluxes observed at two adjacent forest ecosystems located at the southern boundary of European taiga in Russia. The two forests shared similar composition though differing in soil and hydrological conditions. The multi-year observation data indicated that one of the forests was continuously a sink of atmospheric CO<sub>2</sub> while the other a source. By tracking the various C fluxes in the two forest stands with the modeling tool, we tried explaining why the two forests functioned differently regarding their contributions to atmospheric C.

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## 2 Description of study sites

Net ecosystem exchange of carbon (NEE) was measured with eddy covariance technique at two adjacent forested sites in the Central Forest Biosphere Reserve (56°27'N, 32°55'E) at Fyodorovskoe in Tver, Russia from 1999–2004 (Fig. 1). The reserve was established in 1931 possessing an area of 24 447 ha with an elevation of 230–270 m. The forests have been being reserved without any commercial disturbance since the 1960s. The territory of the reserve is far from any industrial or residential areas with little air pollution affecting the forest growth. The two measured sites, the wet and dry spruce forests, are about 2 km apart from each other sharing similar climatic conditions with average annual temperature 3.9°C and precipitation 711 mm for the 1990s (Milyukova et al., 2002).

The wet spruce forest (WSF) site is an old (150 years) spruce forest dominated by spruce (*Picea abies*, 86%) and birch (*Betula pubescens*, 14%). The undergrowth is dominated by *Vaccinium* spp. and *Sphagnum* spp. The above-ground woody biomass is approximately 53 tC ha<sup>-1</sup> (Milyukova et al., 2002). The measurement tower is located in a shallow depression with a heterogeneous territory. The stand has a 60 cm Sphagnum peat layer with the tree roots throughout the whole profile. The soil C content in the peat layer is about 197 ton C ha<sup>-1</sup> (Vygodskaya et al., 2002). The forest is characterized by poor soil aeration, low pH (3.5–3.8) and low nitrogen content (0.5–9.9 kg ha<sup>-1</sup>). The water table is seasonally close or above the soil surface usually in spring. The dry spruce forest (DSF) site is an old (80–150 years) spruce forest with *Picea abies* (53%), *Betula pubescens* (5%), *Populus tremula* (6%), *Ulmus glabra* (6.4%), *Acer platanoides* (18%) and others growing on a well-drained slope. The organic layer is less than 5 cm. The water table is usually at a depth of 1.5 m (Vygodskaya et al., 2004a, 2004b).

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### 3 Measurement of NEE fluxes

The eddy covariance system employed at the experimental sites was similar to that used in the Euroflux project (Aubinet et al., 2000). Briefly, a three-axis sonic anemometer with an omni directional head (Solent R3, Gill Instruments, Lymington, UK) was installed in 29 m height atop aluminum tower. The instrument provides high frequency measurements (20 Hz) of the wind speed and the air temperature. For measurements of CO<sub>2</sub> and water vapor concentration, air was drawn from an inlet atop of the tower through a 1/8" inner diameter BEV-A-LINE tubing to a closed-path infrared gas analyzer (IRGA; LI-COR 6262, Lincoln, NE USA) located close to the bottom of the tower in an insulated wooden shelter. The suction pump was placed in front of the analyzer gas-inlet to ensure the air to be pushed through the instrument with a flow rate of approximately 4-5 l min<sup>-1</sup>. A pressure transducer (PTP101B, Vaisala, Helsinki, Finland) in the reference cell provided the necessary information to correct the measurements for variations associated with pressure fluctuations induced by the pump. The analyzer was run in absolute mode with CO<sub>2</sub> and water-free air circulating in the reference cell, using a combination of magnesium perchlorate and soda-lime. Calibration of the instrument was checked regularly once a week using air of known CO<sub>2</sub> (pressure bottle) and H<sub>2</sub>O (dew-point generator, LI 610, LI-COR, Lincoln, NE USA) concentrations. Output from the sonic anemometer and infrared gas analyzer were read at 20 Hz through RS-232 ports and stored into computers for subsequent analysis.

Ambient CO<sub>2</sub> concentrations at heights of 0.20, 1.0, 2.0, 5.0, 11.0, 15.6, 25.0, 27.6 m were recorded with a system consisting of a LiCor nondispersive infrared gas analyzer (Li-Cor 6251, LI-COR, Lincoln, NE USA), pump (KNF, Neurberger, Germany), switching manifold, BEV-A-Line tubing and datalogger (Campbell, model CR23X). Air was drawn through the tubes at a rate of 7 l min<sup>-1</sup>, with each height being samples for 2 min, with the reading taken at rate of 1 Hz over the last 10 s of sampling at each height and averaged before being stored. The eddy tower was also equipped with instruments to measure environmental factors: incoming photosynthetic photon

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flux density (model LI-190SA, Lincoln, NE USA), humidity and temperature (model HMP35D, Vaisala, Helsinki, Finland), air pressure (model PTB101B, Vaisala, Helsinki, Finland), wind velocity (model A100R, Vector Instruments, UK), total downward and upward radiation (LXG055), and shortwave downward and upward radiation (CM14, Kipp and Zonen, Delft, Holland). Precipitation was collected under the canopy on the height of 1 m above ground and was measured by a tipping bucket rain gauge (model 52202, R.M. Young Company, Traverse City, USA).

Five soil heat flux plates (Rimco HFP-CN3, McVan Instruments, Melbourne, Australia) installed at a depth 4–5 cm were used to obtain an average soil heat flux in the neighborhood of the tower. Soil temperature was measured by sensors PT 100 at two profiles at depths of 5, 15, 50 and 100 cm and then averaged for every depth. All meteorological data were collected every 10 s, and 10 min averages or sums (precipitation only) were stored in the datalogger (DI3000, Delta-T, Burwell, UK). For comparison with half-hourly eddy flux data, 30 min averages of the environmental data were subsequently calculated.

Eddy tower measurements were conducted at WSF and DSF for six years from 1999–2004. A complete dataset of daily NEE fluxes measured at the WSF site were achieved for the entire measurement time span. The multi-year average annual NEE flux for the WSF site was about 2000 kg C ha<sup>-1</sup> per year. However, the observed data at the DSF site were not complete due to malfunctions of the instruments at the site. The continuous measurements at DSF only covered a time period from 27 July 2002 to 15 May 2003. Based on the limited measurements, an average annual NEE flux was estimated as –1440 kg C/ha for DSF (Van der Molen et al., 2007<sup>1</sup>). The observations indicated that the two adjacent forests, WSF and DSF, acted as a source and a sink,

<sup>1</sup> Van der Molen, M. K., Dolman, A. J., Marchesini, L. B., Ciais, P., Corradi, C., Heimann, M., Kuwada, T., Kononov, A. V., Kurbatova, J., Maximov, T., Moors, E., Nakai, T., Schulze, E., Shibistova, O., Ohta, T., Valentini, R., Varlagin, A., Viovy, N., Vygodskaya, N., and Zimov, S.: The carbon balance of the Boreal Eurasia consolidated with eddy covariance observations, *Global Change Biol.*, submitted, 2007.

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respectively, of atmospheric CO<sub>2</sub> (Van der Molen et al., 2007<sup>1</sup>). Water table depths were measured at WSF and DSF in 2004.

#### 4 Validations of Forest-DNDC for spruce forests

Forest-DNDC is a generic forest biogeochemical model. The model was developed by integrating two existing models, an upland forest model PnET-N-DNDC (Li et al., 2000; Stange et al., 2000) and a wetland forest model Wetland-DNDC (Zhang et al., 2002; Li et al., 2004; Cui et al., 2005). Equipped with the upland and wetland features, Forest-DNDC is capable of simulating both aerobic and anaerobic processes at landscape scale. The structure of Forest-DNDC is shown in Fig. 2. Forest-DNDC consists of two components. The first component consisting of the soil climate, plant growth and decomposition sub-models converts the primary drivers (e.g. climate, soil temperature, moisture, pH, Eh and substrate concentration gradients). The second component consisting of the nitrification, denitrification and fermentation sub-models predicts transformations of C and N driven by the soil environmental factors. The six interacting sub-models form a computable framework to simulate the forest growth and soil biogeochemical processes including SOM turnover and emissions of CO<sub>2</sub>, nitrous oxide (N<sub>2</sub>O), nitric oxide (NO), dinitrogen (N<sub>2</sub>) and methane (CH<sub>4</sub>). The modeled NEE flux is the net sum of the simulated photosynthesis (i.e. gross primary production), plant autotrophic respiration and soil microbial heterotrophic respiration. If the simulated ecosystem is an upland forest, a one-dimension hydrological routine will be applied to track the vertical movement of water in the soil profile (Zhang et al., 2002). The soil water flow and moisture will be modeled based on precipitation, evapotranspiration and soil texture. If the simulated ecosystem is a wetland forest, the model will require daily ground water table depth (WT) as an input parameter to define the saturated and unsaturated zones in the modeled soil profile. The input WT data can be obtained from one of three optional sources including (1) field-observed WT, (2) predicted WT

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with empirical equations developed with historical WT data, and (3) predicted WT with spatial distribution hydrological models based on the watershed information (e.g. topography, climate, soil and vegetation). An interface has been built in Forest-DNDC to allow users to select one of the options to define the WT fluctuation.

To test the applicability of Forest-DNDC for spruce forests in temperate or boreal areas, we applied the model for two upland spruce forests in Germany and one in the U.S. where NEE fluxes were measured in 1998, 2001 and 1997, respectively. The two German forests were 20- and 50-years old spruce plantations located at Aberf and Tharandt, respectively (from EUROFLUX database at [http://carbodat.jrc.it/data\\_arch.f.html](http://carbodat.jrc.it/data_arch.f.html)). The U.S. forest was a natural forest (140-years old) dominated by spruce but also contained hemlock and other conifers in the Howland Forest in Main (Hollinger et al., 1999; Xiao et al., 2005). Forest-DNDC was run for the three spruce forests to simulate their daily photosynthesis and ecosystem respiration rates, which were further converted to NEE fluxes. The physiological and phenology parameters of spruce and other relevant tree species utilized in the simulations were originally adopted from Aber and Federer (1992) but slightly modified based on calibration tests against the three spruce forests in Germany and the U.S. The modified parameters included minimum photosynthesis temperature and wood respiration fraction. All the forest parameters adopted in Forest-DNDC for the study are listed in Table 1. Figure 3 shows the modeled NEE fluxes in comparison with observations for the three spruce forests in Germany and the U.S.

Equipped with the calibrated forest parameters, Forest-DNDC was applied for the two Russian spruce forests, WSF and DSF. The daily weather data of 1999–2004 utilized for the 6-year simulations were obtained from the local climatic station at Fyodorovskoe. The forest structure was set to be a 150-years old spruce as the upper-story with a 50-years old birch as the under-story for the Russian sites. The WSF site had a 60 cm organic layer containing about 200 tons C/ha, and the DSF site a 5 cm organic layer containing 25 tons C/ha. The water table data measured in 2004 were repeatedly utilized for each of all the simulated years. Through the simulations, daily and

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annual fluxes of photosynthesis, plant autotrophic respiration, soil heterotrophic respiration and NEE were produced for WSF and DSF for 1999–2004. The modeled daily and annual NEE fluxes were compared with the observed NEE fluxes for the WSF site. The comparison showed that the patterns and magnitudes of the modeled daily NEE fluxes were in agreement with that of the measured NEE fluxes (Fig. 4). The modeled multi-year average annual NEE fluxes were 1800 and  $-2200 \text{ kg C ha}^{-1} \text{ yr}^{-1}$  for WSF and DSF, respectively, which are comparable with the observations (2000 and  $-1440 \text{ kg C ha}^{-1} \text{ yr}^{-1}$  for WSF and DSF, respectively) reported by van der Molen et al. (2007)<sup>1</sup> (Table 2). In agreement with the observations, the modeled results indicated that WSF was a weak source while DSF a weak sink of atmospheric  $\text{CO}_2$ . The modeled data further showed that the forest photosynthesis rates or the plant autotrophic respiration rates between WSF and DSF were close to each other but the soil heterotrophic respiration rates differed between the two forests (Table 3). The results implied that the soil processes, especially the decomposition process, at the WSF site could play a key role in switching the wetland ecosystem from a sink to a source of atmospheric  $\text{CO}_2$ .

## 5 Sensitivity analysis

To test the hypothesis that the decomposition processes in the WSF soil could switch the ecosystem from a sink to a source of atmospheric C, we re-run Forest-DNDC for the WSF case but with varied soil hydrological scenarios. With the 2004-observed daily water table (WT) depth as baseline scenario (WT0), we systematically elevated the daily WT depths by 40 and 20 cm, and also decreased the daily WT depths by 40 and 20 cm. Thus we created four alternative scenarios, WT+40, WT+20, WT–20 and WT–40, respectively. Forest-DNDC was run for WSF with the baseline and alternative WT scenarios for year 2004. Results from the sensitivity test runs indicated that when the WT scenario shifted from the highest (i.e. WT+40) to the lowest (i.e. WT–40) (1) the fraction of soil profile allocated in the unsaturated zone significantly increased

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(Fig. 5), (2) the annual soil heterotrophic respiration rate drastically increased from 315 to 6160 kg C/ha (Fig. 6); and (3) the annual NEE flux increased from -1820 to 3820 kg C/ha (Fig. 7). The results suggested that variation in WT dynamics could significantly alter C balance in the wetland ecosystems by affecting decomposition rate of the organic matter accumulated in the soil profile.

Forest-DNDC simulates not only CO<sub>2</sub> fluxes but also methane (CH<sub>4</sub>) and nitrous oxide (N<sub>2</sub>O) emissions from wetland ecosystems (Li, 2007; Li et al., 2000) that enables us to assess the net greenhouse effect of the changes in climate or management. In this sensitivity test, the changes in the WT scenarios from WT+40 to WT+20, WT0, WT-20 and WT-40 increased N<sub>2</sub>O emissions from 0.08 to 0.45, 1.99, 3.60 and 13.78 kg N ha<sup>-1</sup> yr<sup>-1</sup>, decreased CH<sub>4</sub> emissions from 697 to 563, 64, 24 and 0 kg C ha<sup>-1</sup> yr<sup>-1</sup>, and increased NEE fluxes (i.e. net CO<sub>2</sub> fluxes) from -1820 to -770, 870, 2540 and 3820 kg C ha<sup>-1</sup> yr<sup>-1</sup>, respectively. Since the three greenhouse gases have different warming potentials based on IPCC (1996), the global warming potential (GWP) of each scenario can be calculated as follows:

$$GWP_i = CO_{2i} + N_2O_i \times 310 + CH_{4i} \times 21;$$

$$\text{with } CO_{2i} = C_i \times (44/12)$$

$$N_2O_i = N_i \times (44/28)$$

$$CH_{4i} = C_i \times (16/12)$$

where GWP<sub>*i*</sub> (kg CO<sub>2</sub> equivalent ha<sup>-1</sup> yr<sup>-1</sup>) is the GWP induced by scenario *i*; CO<sub>2*i*</sub>, N<sub>2</sub>O<sub>*i*</sub> and CH<sub>4*i*</sub> are CO<sub>2</sub> flux (kg CO<sub>2</sub> ha<sup>-1</sup> yr<sup>-1</sup>), N<sub>2</sub>O flux (kg N<sub>2</sub>O ha<sup>-1</sup> yr<sup>-1</sup>) and CH<sub>4</sub> flux (kg CH<sub>4</sub> ha<sup>-1</sup> yr<sup>-1</sup>), and C<sub>*i*</sub> and N<sub>*i*</sub> are fluxes in carbon and nitrogen units respectively (kg C ha<sup>-1</sup> yr<sup>-1</sup> and kg N ha<sup>-1</sup> yr<sup>-1</sup>), induced by scenario *i*.

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The calculated GWP values are 12 880, 13 150, 5 930, 11 740 and 20 720 kg CO<sub>2</sub> equivalent ha<sup>-1</sup> yr<sup>-1</sup> for the WT+40, WT+20, WT0, WT-20 and WT-40 scenarios, respectively. The results indicated that water table variation in wetland ecosystems could simultaneously alter emissions of all the three greenhouse gases (i.e. CO<sub>2</sub>, N<sub>2</sub>O and CH<sub>4</sub>) that will draw an impact on global warming more complex than only counting the C balance.

## 6 Discussions

The C loss from wetland ecosystems due to climate change has long been discussed by the research community although case studies on the hypothesis are still sparse. The difficulties in the studies are related to collecting the field data under usually harsh measurement conditions as well as interpreting the field data by integrating a large number of processes driven by climate, forest growth, soil hydrology and soil microbial activities. The six-year NEE measurements at a wetland spruce forest adjacent to a upland spruce forest in Russia provided an unique case for us to observe how the local climate, forest and soil conditions collectively affected the C dynamics between the two forest ecosystems. By adopting a process-based model, Forest-DNDC, in the study, we reproduced the NEE fluxes from the two forests. The modeled results indicated that it was the soil factors (i.e., soil hydrology and soil C storage) that differentiated the two forest ecosystems regarding their contributions to atmospheric CO<sub>2</sub>. Russia possesses a large area of forested wetlands, which mostly contain the thick organic layers. Under the projected scenarios of global warming, these forest ecosystems may suffer dramatic changes in their C storage as well as other trace gas emissions that could send a significant feedback to the global climate. The modeling approach demonstrated in the study could play a key role in interpreting, integrating and extrapolating the field observations that will eventually enhance our capacity for predicting the C exchange between the atmosphere and terrestrial ecosystems.

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**Table 1.** Physiological and phenology parameters for spruce and birch forests adopted in Forest-DNDC.

Parameter	Definition	Spruce	Birch
LeafGeo	Leaf geometry index	1	2
AmaxA	Coefficient for Amax calculation, n mole CO <sub>2</sub> /g/s	9.3	-46
AmaxB	Coefficient for Amax calculation, slope	21.5	71.9
HalfSat	Half saturation light intensity, u mole/m <sup>2</sup> /s	200	200
k	Light attenuation constant	0.5	0.58
PsnTMin	Minimum daytime temperature for Dtemp calculation, degree C	-4.0	4.0
PsnTOpt	Optimum daytime temperature for Dtemp calculation, degree C	24.0	24.0
PsnTMax	Maximum daytime temperature for Dtemp calculation, degree C	45.0	45.0
DVPD1	Coefficient A for DVPD as a function of VPD	0.05	0.05
DVPD2	Coefficient B for DVPD as a function of VPD	2.0	2.0
RespQ10	Effect of temperature on respiration	2.0	2.0
RootMRRespFrc	Ratio of fine root maintenance respiration to biomass production	1.0	1.0
WoodMRFrc	Wood maintenance respiration as a fraction of gross Psn	0.07	0.07
GRespFrac	Growth respiration as fraction of allocation	0.25	0.25
FolReten	Leaf retening time, years	4.0	1.0
SLWmax	Maximum specific leaf weight, g dry matter/m <sup>2</sup> leaf	170	100
GDDFolStart	GDD for leaf to start growth	250	100
GDDFolEnd	GDD to complete foliage production, degree C	1100	900
SenescStart	Julian day to start leaf senescence	270	260
FolNCon	Leaf N concentration by weight	1.2	2.2
FolNRtrans	Fraction of leaf N retranslocated	0.5	0.5
FolCNR	Leaf C/N ratio	37.0	21.0
BaseFolRespFrac	Dark respiration as fraction of Amax	0.075	0.1
AmaxFrac	Daily Amax as fraction of instantaneous Amax	0.76	0.76
PsnTOpt	Optimum temperature for photosynthesis, degree C	24.0	24.0
PlantCReserveFrac	Fraction of available C for plant reserve	0.75	0.75
WoodCNR	Wood C/N ratio	200	180
WUEConst	Water use efficiency constant	13.9	13.9
SLWdel	Specific leaf weight, g dry matter/(m <sup>2</sup> leaf * g foliage mass)	0.0	0.2
FolRelGrowMax	Maximum leaf growth rate, %/yr	0.3	0.95
MinWoodFolRatio	Minimum wood/leaf ratio	1.25	1.4
GDDWoodStart	GDD for wood to start growth	250	100
GDDWoodEnd	GDD for wood to end growth	1400	900

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**Table 2.** Characteristics of five spruce forest stands used for validation of Forest-DNDC.

Stand	Aberf, Germany	Tharandt, Germany	Howland, USA	Fyodorovskoe, Tver, Russia	Fyodorovskoe, Tver, Russia
Location	56.6	51	45°12' N	56	56
Age, yrs	20	50	140	150	150
Dominant species	Spruce plantation	Spruce plantation	Red spruce, hemlock	Spruce, birch	Spruce, birch
Soil	Sandy clay loam, acid	Loam, acid	Sandy loam, acid	Sandy clay loam, acid	Sandy clay loam, acid
Land type	Upland	Upland	Upland	Upland	Wetland
Observed multi-year average NEE, kg C ha <sup>-1</sup> yr <sup>-1</sup>	-5830	-5011	-2577	-1440	2000
Modeled multi-year average NEE, kg C ha <sup>-1</sup> yr <sup>-1</sup>	-5470	-3570	-2280	-2200	1800

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**Table 3.** Modeled C fluxes for the wet spruce forest (WSF) and the dry spruce forest (DSF) in Fyodorovskoe, Tver, Russia in 2004.

Stand	GPP (kg C ha <sup>-1</sup> yr <sup>-1</sup> )	Plant respiration (kg C ha <sup>-1</sup> yr <sup>-1</sup> )	Soil microbial respiration (kg C ha <sup>-1</sup> yr <sup>-1</sup> )	NEE (kg C ha <sup>-1</sup> yr <sup>-1</sup> )
WSF	13295	12895	1342	942
DSF	13297	12334	787	-176

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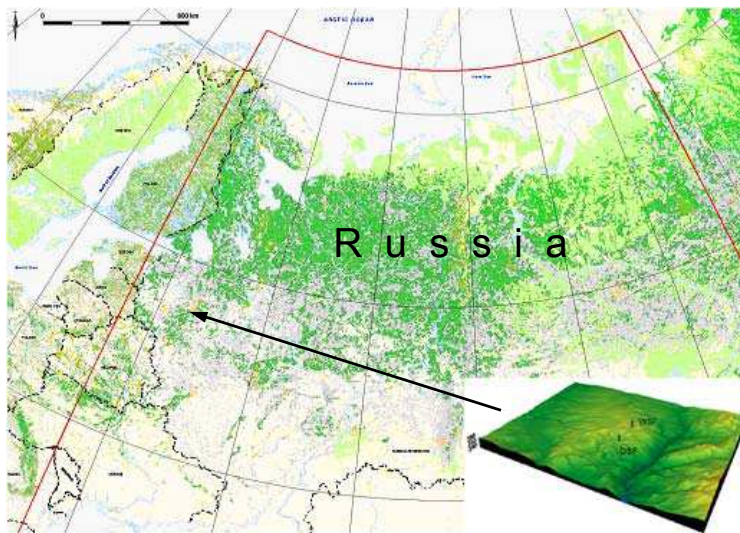
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**Fig. 1.** Location of the Central Forest Biosphere Reserve at Fyodorovskoe in Tver, Russia.

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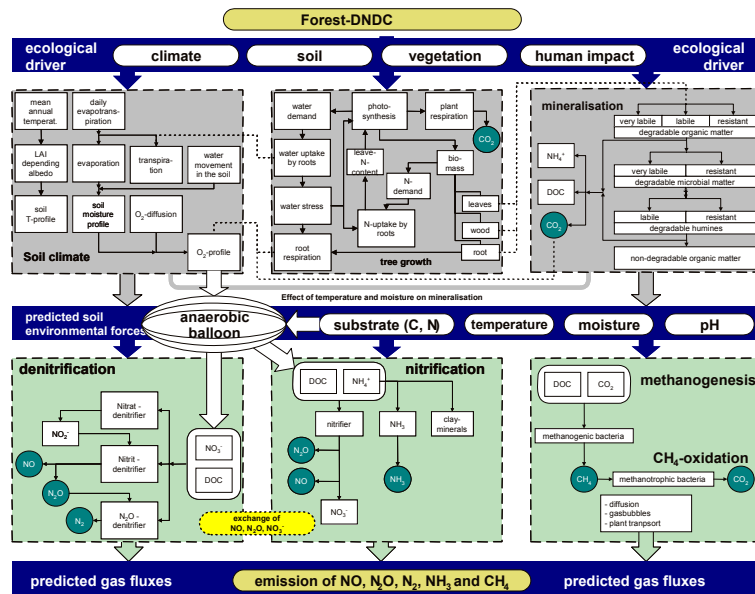


Fig. 2. Structure of the Forest-DNDC model.

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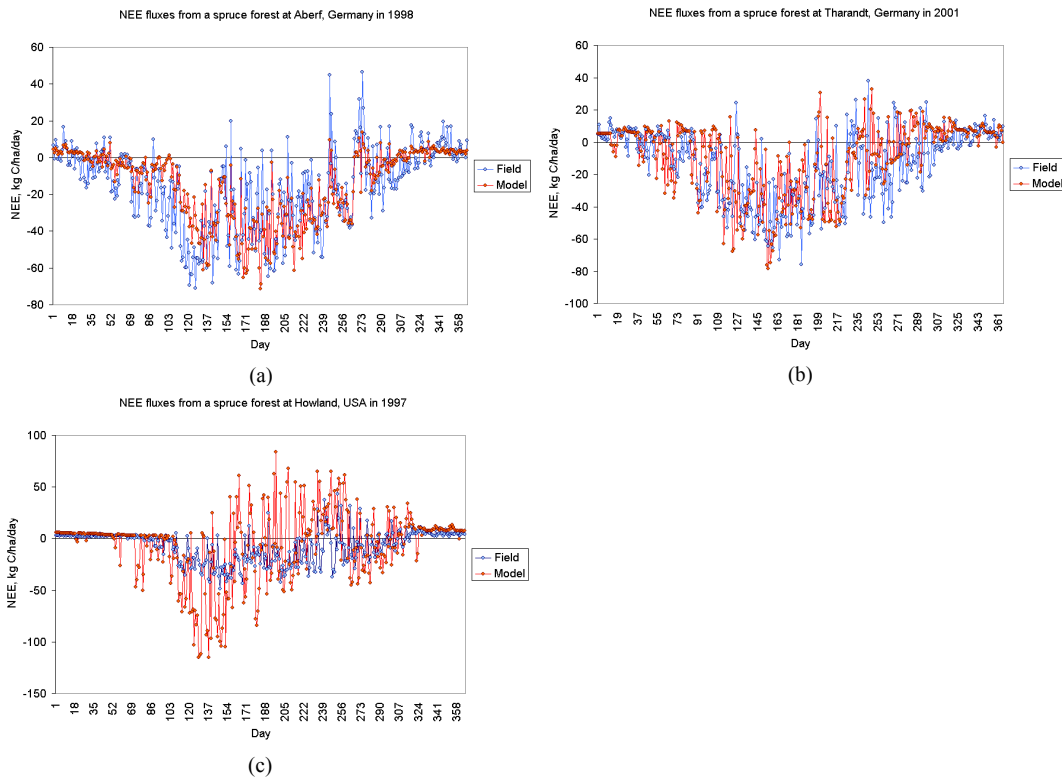
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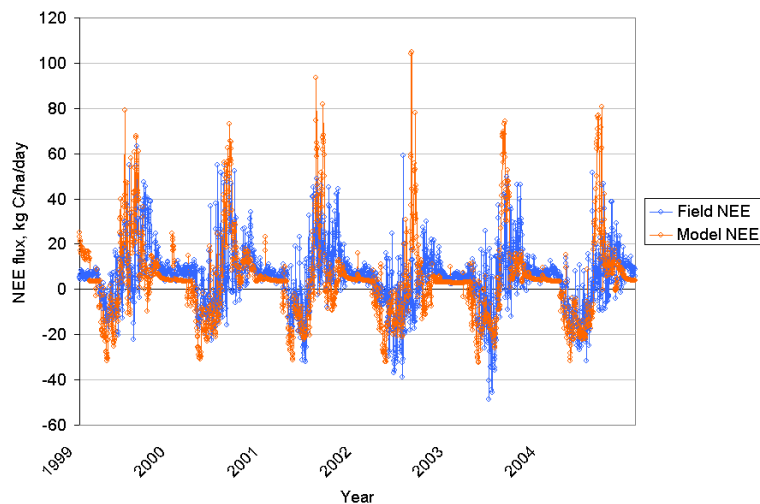


**Fig. 3.** Comparison between observed and Forest-DNDC modeled NEE fluxes for three spruce forest stands in Germany (a) and (b), and the U.S. (c).

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**Fig. 4.** Comparison between observed and Forest-DNDC modeled NEE fluxes from a wet spruce forest (WSF) in the Central Forest Reserve at Fyodorovskoe, Tver, Russia in 1999–2004.

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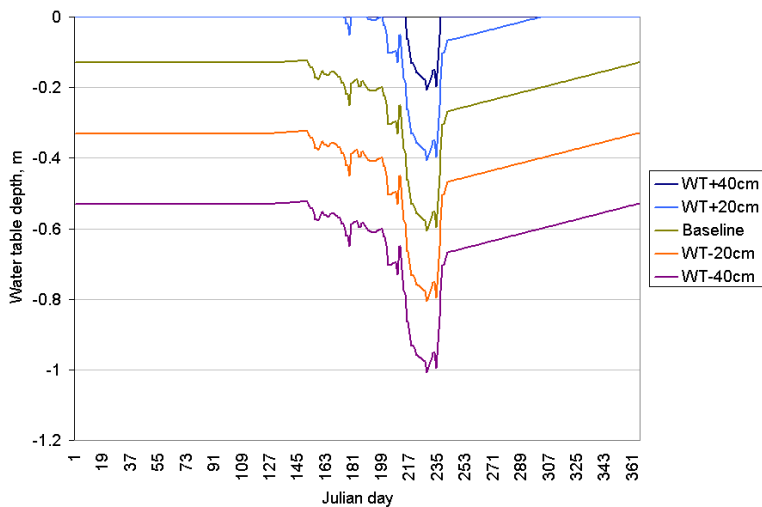


Fig. 5. Daily water table (WT) depths with different WT scenarios at the wetland spruce forest (WSF) in Fyodorovskoe, Russia in 2004.

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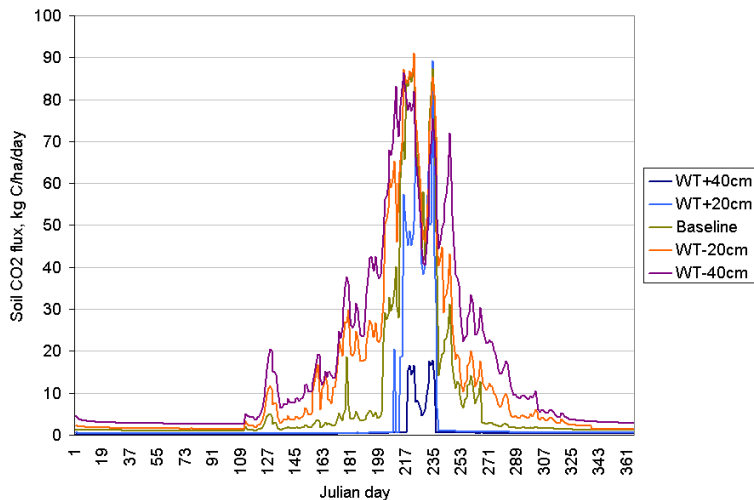


Fig. 6. Modeled daily soil CO2 fluxes from the wetland spruce forest (WSF) with different water table scenarios in Fyodorovskoe, Russia in 2004.

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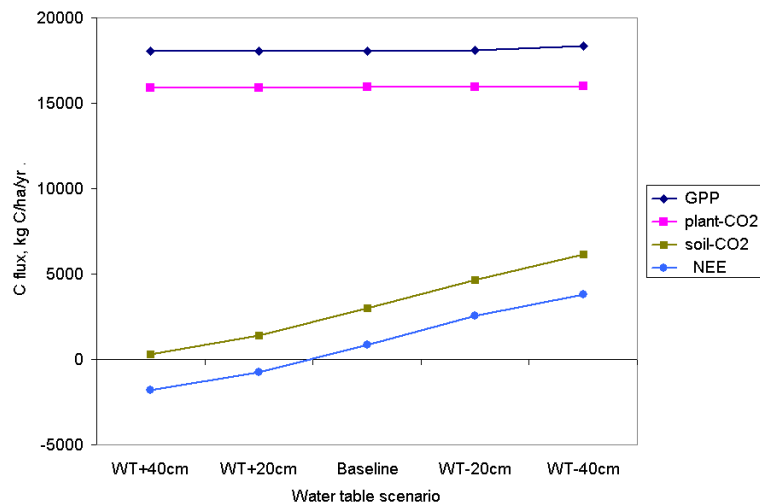
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**Fig. 7.** Modeled annual GPP, plant autotrophic respiration, soil heterotrophic respiration and NEE fluxes for the wetland spruce forest (WSF) with different water table scenarios in Fyodorovskoe, Russia in 2004.

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