

Network environment analysis of a model of carbon flows in a peat bog and fen

A.V. Naumov, N.P. Kosykh, N.P. Mironycheva-Tokareva

Institute of Soil Science and Agrochemistry SB RAS, Novosibirsk, Russia

SUMMARY

- (1) The wide distribution of peat bogs and the ecological problems made by environmental change makes it important to understand their functioning. This article uses a dynamic mathematical model of the carbon transfers in a mire located in the forest-steppe zone of West Siberia.
- (2) We apply this approach to a raised bog and to a fen. We use measured values of the amount of carbon in the six compartments of the model, and of the transfer rates among the compartments. A stationary (steady) state is reached after 200 years or so, but the amounts in the compartments then differ quite a lot from those at the start. We consider possible reasons for these differences.

KEY WORDS: biological turnover, C-flows and storages, modelling, sphagnum bog

Abbreviation	Meaning	Details
PSS (bog)	Pine - dwarf shrub - sphagnum community with scattered birch	Methods
MCS (fen)	Mesotrophic sedge - sphagnum fen	Methods
NPP	Net primary production	Methods
ANP	Above-ground production	Methods
BNP	Below-ground production	Methods
X _n	Compartment n in the model; n = 1 to 6	Table 1
X ₂ [†] _{grn}	Compartment 2 excluding the contribution of trees	Methods
k _{ij}	Rate constant for flow from compartment i to compartment j	Table 1
NEA	Network Environment Analysis	Introduction
SA	Sensitivity Analysis	Results
S	Sensitivity Index	Methods
FCI	Flow Cycle Index	Results
SCI	Storage-based Cycling Index	Results
CAS	Complex Adaptive System	Discussion

INTRODUCTION

Peat bogs are widespread in the Northern Hemisphere. They cover about 4 million km² and contain 500 ± 100 Gt of carbon in peat (Joosten & Clarke 2002, Yu 2012). Carbon in peat makes up approximately 25–30 % of all carbon in soil organic matter (Post *et al.* 1982, Batjes 1996). Northern peatlands play a significant role in the bio-

geochemical cycle of this element in the biosphere, affecting atmospheric CO₂ accumulation and peat mineralisation. The basal age of many peat deposits in northern peatlands is several thousand years, which indicates their long-term stable functioning. Today, in relation to forecasts of global environmental changes, it is important to have reliable substantiation of the development dynamics and stability of these natural ecosystems.



Carbon cycle research on mire ecosystems is complicated by the variety of conditions in which peat has formed and developed, by the variety of modern functional conditions, and by the remoteness and inaccessibility of examples for ground measurements. The mire as a natural ecosystem is characterised by specific structural and functional organisation. Modelling of mire ecosystems can allow us to present the object of study in a standardised form, taking into account a variety of direct and inverse relationships among the components of the system. Analysis of the functional state of the modelled object in the space of environmental factors makes it possible to assess properties and characteristics of a particular natural ecosystem that are not available for field observation.

The development of conceptual and mathematical models of mire ecosystems is relevant for a deeper understanding of current carbon exchange processes at regional and global scales, and for forecasts. Currently, there are two fundamentally different directions in modelling the carbon dynamics of peat bogs.

The first approach uses as a conceptual basis the two-layer structural and functional organisation of peat deposits, as presented in the works of Russian researchers of the mid-20th century (Lopatin 1949, Ivanov 1953, Romanov 1961). It took more than 20 years for the ecological essence of the two-layer hypothesis to be further used in the development of mire ecosystem models, for which Ingram (1978) developed a terminology. The earliest realistic mathematical models of peatland growth were presented by Clymo (1978, 1984, 1992). Subsequently, updated models became widely used for local and regional estimates of the rate of carbon accumulation in bogs (Beilman *et al.* 2001, Borren *et al.* 2004, Borren 2007). A two-layer peat deposit structure and a modified exponential form for peat-addition rates were used to study the cumulative peat mass - age profile of continental mires in Western Canada (Yu *et al.* 2001a). More complex models of long-term peat accumulation included single and double negative exponential decay functions, effective moisture and groundwater depth, as well as plant and litter addition (Clymo 1992, Winston 1994, Hilbert *et al.* 2000, Froelking *et al.* 2001, Yu *et al.* 2001b, Zhang *et al.* 2002). Interesting profile studies of dissolved carbon dioxide, methane and organic carbon were made in a 7 m deep raised bog (Clymo & Bryant 2008). This is not an exhaustive list of the publications, but serves to characterise the direction of studies of the processes of long-term carbon accumulation in peat.

The second direction in modelling carbon dynamics in mire ecosystems is based on system-wide ecological principles (Hannon 1973, Patten 1978, Fath & Patten 1999, Fath *et al.* 2007). In this approach the structure of the ecosystem is understood as the set of (all) components involved in carbon exchange, interconnected by numerous direct and indirect links. Thus, the functional state of the ecosystem at any time is characterised by the carbon reserve (resource) in each component and the rates of incoming and outgoing flows. Any substances, energy or chemical elements can be used as resources, depending on the task set by the researcher. The analysis of such structural and functional relationships within the ecosystem was named 'network environment analysis', NEA (Fath & Patten 1999). The principles of construction of dynamic mathematical models of trophic chains, based on storage - flow diagrams, were considered by Svirezhev (1997) and by Svirezhev & Logofet (1978).

There are few dynamic models of the biogeochemical carbon cycle in mire ecosystems, although mathematical models based on some general properties of the trophic structure of a transition fen have been considered (Logofet & Alexandrov 1984a,b; Zavalishin & Logofet 2001, Zavalishin 2008). We believe that the development of local dynamic models of the carbon cycle of mire ecosystems based on storage - flow diagrams remains relevant, because it gives the researcher tools for developing a deeper and more strictly grounded judgment about functional mechanisms.

The aim of the study we report here was to develop a new conceptual and dynamic mathematical model of the carbon cycle of the mire ecosystem, and to make a short-term forecast of the dynamics of peat bogs of the forest-steppe zone in Western Siberia.

METHODS

Study sites

We worked on the raised sphagnum bog "Nikolaevsky ryam" (55.15° N, 79.04° E), which is located about 270 km west of Novosibirsk. It forms an isolated largely tree-covered mound 1.7 km in diameter in the centre of a 10 km wide valley. The domed peat deposit occupies an area of 2.7 km² and the peat thickness in its central part is about 4.5 m. According to preliminary information the age of the bog is approximately 2600 years (Stepanova & Volkova 2017). The vegetation is a pine+dwaf-shrub+sphagnum community with scattered birch

(PSS, bog) that occupies almost 80 % of the bog area. The height of the tree layer was up to 6–8 metres (*Pinus sylvestris* L. + some *Betula pubescens* Ehrh.). The microrelief was hummocky. The composition of the shrub layer (%) was: *Ledum palustre* L. (40 %), *Chamaedaphne calyculata* (L.) Moench (20), *Vaccinium vitis-idaea* L. (10), *Andromeda polifolia* L. (5), *Oxycoccus palustris* Pers. (3), and *Oxycoccus microcarpus* Turcz. ex Rupr. (2 %). Herbs had trivial cover. The moss cover was represented by: *Sphagnum fuscum* (Schimp.) Klinggr. (60 %), *S. capillifolium* (Ehrh.) Hedw. (30), *S. angustifolium* (Russ. ex Russ.) C.Jens. + *S. magellanicum* Brid. (9), and *Polytrichum strictum* Brid. (1 %).

At a distance of 350–400 metres south-west of the summit of the bog there was a small intra-mire lake, ringed by a 30–40 m wide transition from PSS bog to lake, occupied by mesotrophic sedge-sphagnum fen vegetation (MCS, fen). The peat deposit there was about 3.5 m thick. Sedges such as *Carex rostrata* Stokes, *C. lasiocarpa* Ehrh., *C. limosa* L., *Eriophorum vaginatum* L., and small dwarf shrubs including *Andromeda polifolia* and *Oxycoccus palustris*, were present here. The cover of *Sphagnum fallax* (Klinggr.) Klinggr., *S. riparium* Ångstr. was patchy. In summer the mire water table fluctuated 10–12 cm below the surface formed by the sphagnum capitula. The mire complex was surrounded by highly productive reed and sedge-reed eutrophic fens.

Description of the model

In development of the mathematical model, we proceeded from the most common views about trophic network structure in mire ecosystems, which supports carbon dioxide flow from the atmosphere to primary producers, provides the movement of carbon along the trophic chain, and releases this biogenic chemical element into the environment.

We assumed that carbon in a mire ecosystem is

distributed between six basic compartments (Figures 1, A1, A2) defined by position, structure, or function (or some combination of these):

$X1_{\text{air}}$: C content of a ground layer of air up to an arbitrary 1 m high: a source and sink for the whole system;

$X2_{\text{gm}}$: above-ground phytomass;

$X3_{\text{rs}}$: underground organs of plants;

$X4_{\text{acr}}$: dead plant parts and peat in the acrotelm;

$X5_{\text{cat}}$: peat in the catotelm; and

$X6_{\text{DOC}}$: organic matter, and carbon dioxide and methane dissolved in bog water.

The surface layer of the atmosphere plays an important role in the functioning of the mire ecosystem. Carbon dioxide, released in the processes of respiration and mineralisation, enters compartment $X1$ and is again involved (reutilisation) in metabolic processes. The same applies to methane. In fact, the net primary production NPP of the ecosystem is largely generated by internal processes of reutilisation (Naumov 2004, 2009). In the presented version of the model, we do not distinguish processes involving methane. We leave this question for future publications.

Compartment $X4_{\text{acr}}$ includes all dead plant parts, litter and peat in the acrotelm. Carbon stocks in compartments X_i ($i=1\dots6$) characterise the state of the ecosystem at any given time and have dimensions ML^{-2} (units, g m^{-2}). Carbon flows in the mire ecosystems are shown by arrows in the diagram and flows have dimensions $\text{ML}^{-2}\text{T}^{-1}$ (units, $\text{g m}^{-2} \text{yr}^{-1}$):

$q1, q6$: carbon feed from the environment;

$y1, y6$: carbon output from mire ecosystem;

f_{ij} : carbon flows between the links of the trophic network;

k_{ij} : corresponding kinetic constants of metabolic processes, $i=1\dots6, j=1\dots6$ (Table 1).

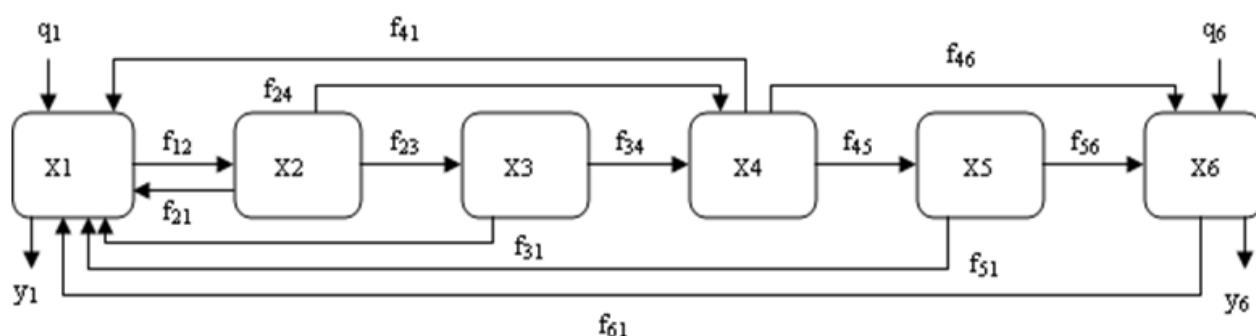


Figure 1. Storage – flow diagram of a mire ecosystem; see Table 1 for details of amounts ('X?') and flows ('f??').

The dynamics of carbon stocks in the compartments of the mire ecosystems was described by the following system of differential equations (balance approach):

$$dX_{1\text{air}}/dt = q_1 - y_1 - f_{12} + f_{21} + f_{31} + f_{41} + f_{51} + f_{61}$$

$$dX_{2\text{grn}}/dt = f_{12} - f_{21} - f_{23} - f_{24}$$

$$dX_{3\text{rts}}/dt = f_{23} - f_{31} - f_{34}$$

$$dX_{4\text{acr}}/dt = f_{24} + f_{34} - f_{41} - f_{45} - f_{46}$$

$$dX_{5\text{cat}}/dt = f_{45} - f_{51} - f_{56}$$

$$dX_{6\text{DOC}}/dt = q_6 - y_6 + f_{46} + f_{56} - f_{61}.$$

We made some assumptions in developing this model.

Assumption 1: external conditions are stable and do not materially affect mire ecosystem dynamics. First of all, we were interested in the internal (endogenous) mechanism of support and functioning of the carbon cycle in stable external conditions.

Assumption 2: flow between two compartments is a linear function of the carbon reserve in the donor compartment (donor type), $f_{ij} = k_{ij} \cdot X_i$ ($i = 1 \dots 6$, $j = 1 \dots 6$), where k_{ij} are rate constants of the respective processes. Carbon flows leaving the mire ecosystem also belong to the donor type: $y_1 = k_{10} \cdot X_{1\text{air}}$, $y_6 = k_{60} \cdot X_{6\text{DOC}}$.

Table 1. Variables and parameters of the model for ‘Pine-dwarf shrub-sphagnum bog’ (PSS), and ‘mesotrophic sedge-sphagnum fen’ (MCS) communities.

Variable or parameter description		Ecosystem	
		PSS bog	MCS fen
Initial stock of C (g m⁻²)			
$X_{1\text{air}}$	The surface layer of the atmosphere to a height of 1 metre	0.16	0.16
$X_{2\text{grn}}^{\dagger}$	Live above-ground phytomass	426 [†]	343
$X_{3\text{rts}}$	Live underground plant organs (roots, rhizomes etc.)	1542	1795
$X_{4\text{acr}}$	Dead plant residues and peat (acrotelm)	2020	2300
$X_{5\text{cat}}$	Peat (catotelm)	246000	90750
$X_{6\text{DOC}}$	Dissolved organic compounds, carbon dioxide and methane	240	200
External flow of C (g m⁻² yr⁻¹)			
q_1	CO ₂ feed from atmosphere	16	10
q_6	Dissolved carbon input	0	10
y_1	CO ₂ emission into the ambient space	0	0
y_6	Dissolved carbon output	14.4	4
Process kinetic constants (yr⁻¹)			
k_{12}^{\wedge}	Photosynthesis, CO ₂ assimilation by plant cover	2018	1480
k_{21}	Respiration of above-ground phytomass	0.15	0.30
k_{23}	Carbon translocation into the underground plant organs	0.57	0.72
k_{24}	Dying of above-ground phytomass	0.15	0.23
k_{31}	Respiration of underground plant organs	0.30	0.30
k_{34}	Dying of underground plant organs	0.27	0.40
k_{41}	Mineralisation (decomposition) of dead plant residues	0.006	0.006
k_{45}	Biotransformation of dead plant residues into peat	0.20	0.20
k_{46}	Dissolution of organic compounds and formed C-gases	0.03	0.03
k_{51}	Peat mineralisation	0.0005	0.001
k_{56}	Dissolution of organic compounds and formed C-gases	0	0
k_{61}	Mineralisation of dissolved organic compounds and degassing of bog water	0.01	0.10

[†] Excluding the contribution of free-standing trees.

[^] The two digits after the ‘*k*’ refer to flow between the numbered *X*-compartments.

Assumption 3: $q_1 = \text{constant}$, $q_6 = \text{constant}$.

Assumption 4: values of the parameter k_{ij} are specific to each type of mire ecosystem and have been determined by evolution.

Our assumption of the linearity of relationships between network compartments was based on the ecological linearisation hypothesis (Patten 1975), according to which ecosystems rich in feedback interconnections are linearised by feedback elements that may be linear, nonlinear or stochastic (Patten 1975). Strong non-linear relationships between the participants of biological turnover would apparently be more probable under a transient regime of functioning and permanent structural perturbation of the trophic network in the course of succession. Such perturbation may be equivalent to “catastrophe” for the initial ecosystem.

Estimating the ‘X’ and ‘k’ variables and parameters of the model

We used net primary productivity data, rates of CO_2 gas exchange, reserves of live above-ground and underground phytomass, dead plant residues, decomposition (mineralisation) of dead plant residues and peat, carbon dioxide and methane emissions obtained in laboratory and field studies during 2008–2016 in the raised sphagnum bogs of the forest-steppe zone (Western Siberia) (Kosykh 2009, Naumov *et al.* 2009, Naumov 2011, Naumov & Kosykh 2011, Mironycheva-Tokareva *et al.* 2017, Naumov 2017, Kosykh 2018).

We used generalised parameter estimates in the simulation (Table 1). Initial values of carbon stocks in above-ground and underground parts of plants, dead plant residues (on the surface and in peat to a depth of 30 cm) are averaged estimates of field data for the observation period. Above-ground phytomass was measured by clipping on 10 plots of 0.5×0.5 m in each ecosystem. These samples were sorted into living and dead parts of shrubs, dwarf shrubs and herbs. Dry plant residues on these plots were measured too. Above-ground tree biomass was not included in the calculations. The choice of the initial estimate of the variable $X_{2\text{gm}}^+$, with superscript ‘+’ indicating without the contribution of the trees, is appropriate for comparing PSS bog with a treeless MCS fen. This approach allowed us to compare (on the same basis) the rates of peat formation in two mires with different tree tiers. We consider the tree stand as an environmental factor rather than as a participant in peat formation. NPP of trees (in terms of carbon) was $24 \text{ g m}^{-2} \text{ year}^{-1}$, C pool of needles 60 g m^{-2} , and the stock of wood 170 g m^{-2} (Mironycheva-Tokareva *et al.* 2017). Below we consider the effect of these estimates on the simulation results.

The reserves of mosses and living underground plant organs, including tree roots, were determined on the same quadrats by excavating monoliths (10×10 cm) to a depth of 30 cm. Each sample was separated into the fractions: living underground plant organs, peat, and plant debris. Sphagnum capitula were cut off as part of the living above-ground phytomass. All fractions were dried and weighed. Carbon was assumed to form 50 % of the dry mass. The initial carbon content in the surface air was calculated on the basis of numerous measurements (by infra-red gas analyser) of the concentration of carbon dioxide. The initial pool of carbon dissolved in bog water (organic compounds, CO_2 and CH_4) was estimated conditionally on the basis of one-time measurements in a layer of 0–140 cm. The concentration of DOC in $X_{6\text{DOC}}$ was measured by optical density (Efremova *et al.* 2014). Dissolved gases CH_4 and CO_2 were analysed on a gas chromatograph after they were displaced by argon.

Annual increments of live phytomass fractions were used to calculate net primary production. The above- and below-ground estimates of NPP (mosses, grasses, shrubs and dwarf shrubs) averaged over several seasons were used to calculate photo assimilation parameters taking into account plant respiration. The rates of net CO_2 assimilation and total respiration were measured by a closed chamber method using an infrared gas analyser. We believed that the biomass created in the current season did not accumulate in the ecosystem, but completely died off, i.e. $f_{24} = \text{ANP}$, $f_{34} = \text{BNP}$. Kinetic constants of the corresponding processes were calculated taking into account the size of the carbon pool of the donor compartment and the current estimation of the carbon flux. The rate constants k_{21} and k_{31} were calculated on the basis of averaged estimates of the respiration rate of grasses, shrubs, dwarf shrubs and sphagnum mosses obtained in field and laboratory experiments.

In accordance with the hypothesis of the two-layer structure of peat deposits, we included compartments $X_{4\text{acr}}$ and $X_{5\text{cat}}$, respectively, as acrotelm and catotelm, in the model. The $X_{4\text{acr}}$ carbon pool included all dead plant matter on the surface, plus peat and plant residues to a depth of 30 cm. The $X_{5\text{cat}}$ carbon stock was estimated taking into account the bulk density of the peat and the deposit depth without the top 30 cm layer. The plant residues and peat decomposition rates in acrotelm and catotelm were determined in laboratory incubation experiments at 3–4 °C (Naumov 2017). The flow f_{61} was calculated by a diffusion method from the concentrations of dissolved carbon dioxide and methane in peat water (Naumov 2009, 2011). The kinetic constant k_{61} was found from the quotient $f_{61}/X_{6\text{DOC}}$.

Dead plant residues transform to peat and produce water-soluble organic compounds DOC, which move down the profile with water flows. We assume that the dissolution of peat organic compounds in the deeper layers is negligible ($f_{56} = 0$). This assumption is based on the results of radiocarbon studies of the peatland profile, which indicate a younger age of DOC relative to peat (Chanton *et al.* 2008, Clymo & Bryant 2008). Estimates of external flows q_1 , q_6 , y_1 , y_6 in Table 1 are indicative. We consider later the influence of these on the functional state of the carbon cycle of the simulated mire ecosystems.

Simulation modelling

Numerical solution of the system of differential equations of the presented model was performed using the software complex EcoNet 2.2 online (see Appendix). The EcoNet service was accessible through its web interface (<http://eco.engr.uga.edu/>). The software, terms and conditions of its use, peculiarities of initial data preparation, and information about environment analysis are described in detail in the developer's manual (Kazanci 2007). Our simulation programs are shown in the Appendix. NEA (Network Environment Analysis) is used to quantify the actual relationships between compartments, ecological inputs and outputs, and to calculate the steady state carbon pools of the ecosystem compartments (X_i). This approach treats the system as a whole and provides an elegant way to quantify the effects of all direct and indirect flows in the system. The result of this analysis is a series of scalar and matrix values representing various compartmental and system-wide properties (Appendix). Variable and parameter values for numerical modelling of the states of the mire ecosystem's carbon cycle in PSS bog and MCS fen are presented in Table 1.

Model sensitivity to variation of input values was assessed by the sensitivity index S , which was calculated using: $S_i = 100 \cdot (X_i - X_i^{\text{new}}) / X_i$, $i = 1 \dots 6$. Positive S values indicated decrease of carbon reserves in compartments, and negative values indicated growth of reserves, in response to the change of an initial input value.

RESULTS

Simulation and environmental analysis

Both the mire ecosystems PSS bog and MCS fen formed under the same climate conditions and were linked by biogeochemical flows within a single mire complex. At the same time they differ in terms of type of solute supply, plant species and water regime. It is

obvious that these differences had a significant effect on the functional and carbon states of these ecosystems. This choice of study site allowed us to assess the effectiveness of our model of the carbon cycle, in calculating basic variables and parameters in steady state conditions, for both ecosystems. We can thus assess the functional stability of the mire ecosystem's carbon biogeochemical cycle under current conditions.

The model (as a system of differential equations) had an asymptotically stable stationary state (Figures 2, 3, 4) in both bog and in fen systems. The time course of compartment carbon storages reflects the most probable behaviour of these mire ecosystems under almost constant external environmental factors. We used the time-course plot and throughflow values to see how close the system is to a steady-state. For a steady-state model, flow into compartment X_i should be very close to flow out of that compartment at the end of the simulation (Appendix). The simulation showed (Figures 2, 3, 4) that the flows were relatively quickly aligned (180–200 years) in almost all compartments, except $X_{5\text{cat}}$ in MCS fen (Figure 2). The raised bog (PSS bog) after the transition to a stationary state will partly support the accumulation of peat in the MCS fen through the long-term flow from the bog of dissolved C at a rate of $6.7 \text{ g m}^{-2} \text{ year}^{-1}$ (Appendix). According to preliminary estimates, the tree stand could increase the initial carbon stocks in compartments $X_{2\text{grn}}$, $X_{3\text{rts}}$ and $X_{4\text{acr}}$ by 10–15 % in PSS bog. However, such amendments did not affect the structure of the model and did not lead to the redistribution of carbon pools in the stationary state.

There is still no clear answer to the important question: are modern peat bogs a source or a sink of atmospheric CO_2 ? The uncertainty of the answer is because the dynamics of the carbon balance of mire ecosystems responds to changes in environmental factors.

To study this, we introduced the state variable $X_{1\text{air}}$ into the model as a pool of carbon in the 1 m deep surface layer of the atmosphere. The calculations showed that change of CO_2 -C content in compartment $X_{1\text{air}}$ by 2–4 times did not have a significant effect on the steady-state values of $X_{1\text{air}}$, $X_{2\text{grn}}$, ..., $X_{6\text{DOC}}$ when other conditions were stable. Obviously, the effect of increased CO_2 concentration in the atmosphere may be expressed through functional dependence of the photosynthesis rate constant k_{12} on variable $X_{1\text{air}}$, $k_{12} = f(X_{1\text{air}})$.

Steady-state values of $X_{2\text{grn}}$, $X_{3\text{rts}}$, $X_{4\text{acr}}$ were below the initial measured values. The differences (as %) in PSS bog and MCS fen, were 18.1 and 34.7 for above-ground phytomass, 77.4 and 87.2 for

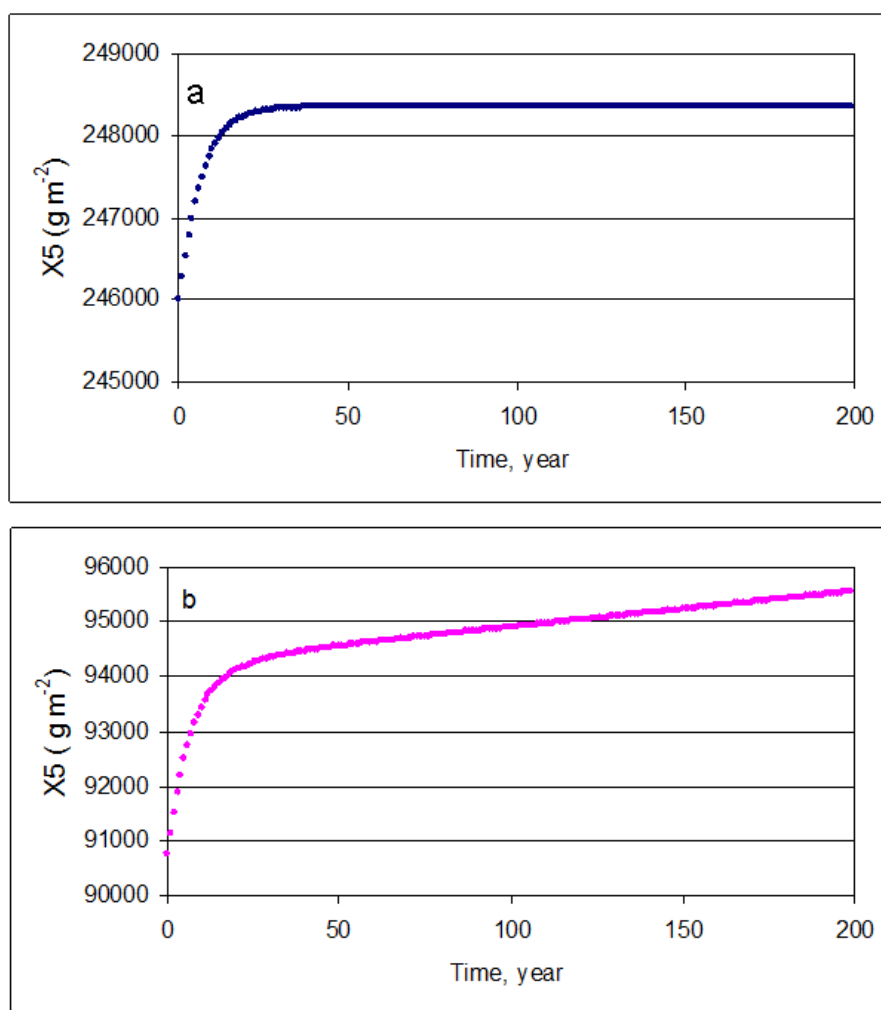


Figure 2. Time-course of $X5_{cat}$ values for PSS bog (a) and MCS fen (b).

underground plant organs, 69.0 and 73.6 for dead plant residues (Figures 3, 4; Appendix). A downward trend in carbon stocks $X2_{gm}^+$ to $X4_{acr}$ is most likely in the near future. The carbon stocks in peat (Figure 2, Appendix) will increase by 1.0 % in PSS bog and by 6.4 % in MCS fen during the next 200 years, according to the model forecast.

Plant composition had a direct effect on carbon turnover rate. Carbon throughflow, T_i , is a measure of activity in the i -th compartment. It sums what goes into (+) the compartment and what comes out (-) of it. This does not bias the accumulation of X_i reserve. Carbon turnover rate was assessed by the residence time (RT) in the compartment at the end of modelling: $RT = X_i / T_i$. Mesotrophic fen MCS was characterised by higher carbon turnover rates (Appendix) compared with ombrotrophic bog PSS, except in the compartment $X4_{acr}$. Thus, carbon in PSS bog peat will renew within 2000 years, and in MCS fen it will renew within 1000 years. The carbon reserve $X4_{acr}$ in steady-state conditions in both mire ecosystems will

renew within 4.2 years (Appendix). Compartment $X4_{acr}$ is an important link in the biogeochemical carbon cycle of mire ecosystems, responsible for the accumulation of carbon in peat. It would be useful to continue a detailed study of this issue.

The total throughput of the system (Appendix), as a sum of T_i , is higher in the raised PSS bog than in the mesotrophic MCS fen. The flow matrix **F** represents the overall picture of the connections between the compartments in the steady state. The elements of the **F**_{ij} matrix are estimates of the annual carbon flow from compartment j to compartment i . Gross photosynthesis in PSS bog (f_{21}) will be higher than in MCS fen in the steady state after 200 years (300 and 240 $g\ m^{-2}\ year^{-1}$, respectively, Appendix). About 50 % of the total carbon emission returned into $X1_{air}$ through plant respiration ($f_{21} + f_{31}$); while the rest was from mineralisation of plant residues, peat and dissolved organic compounds, and from degassing: 130 (PSS bog) and 120 (MCS fen) $g\ m^{-2}\ year^{-1}$ (Appendix).

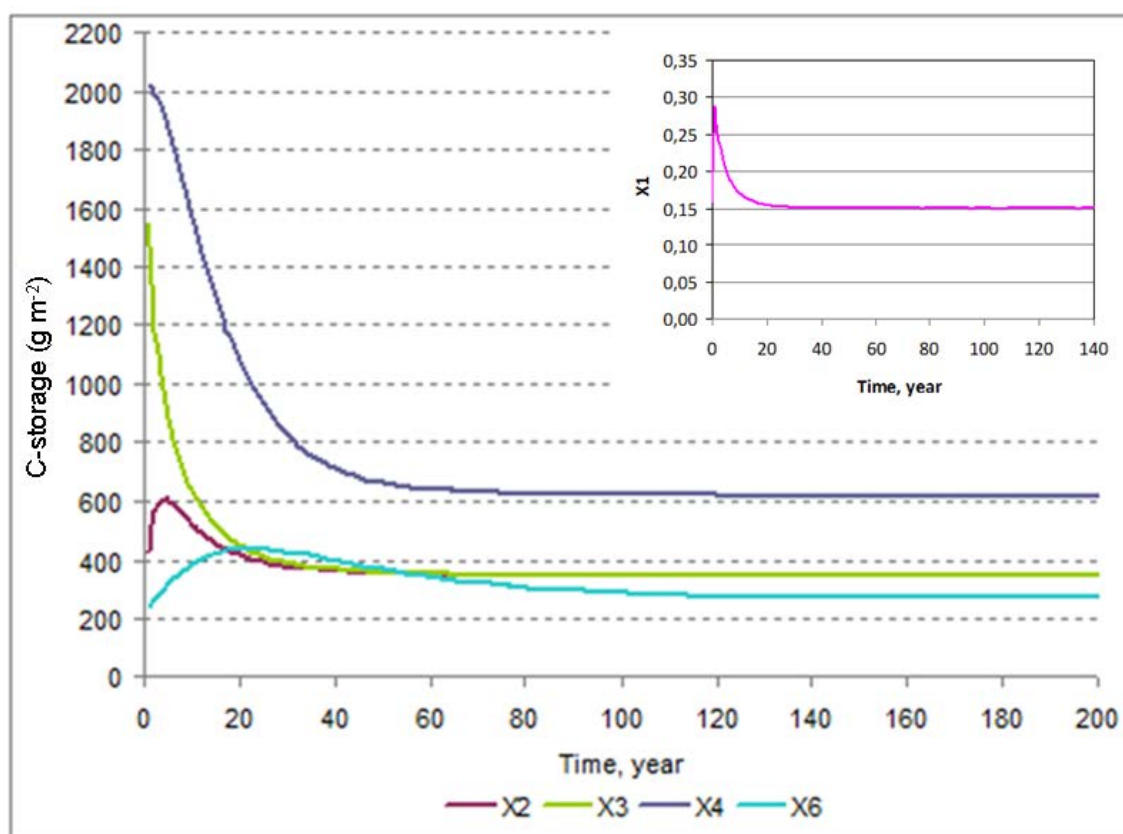


Figure 3. Time-course of X1–X4 and X6 compartment storage values in PSS bog.

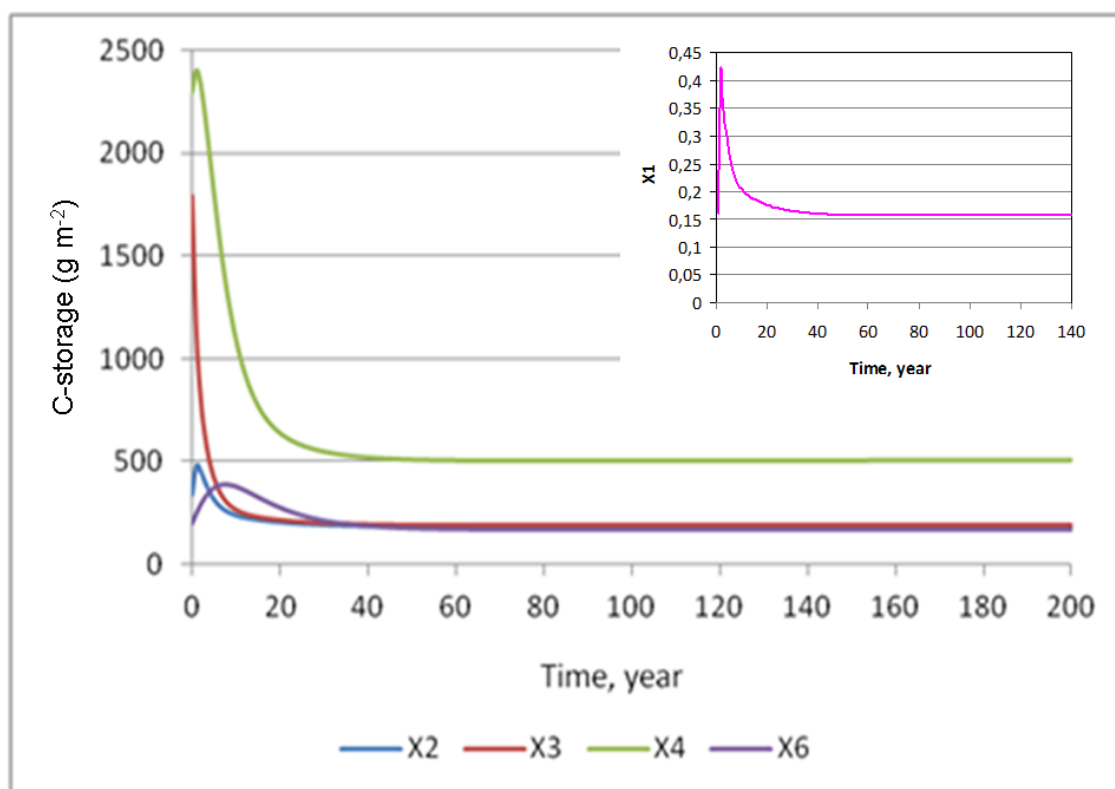


Figure 4. Time-course of X1–X4 and X6 compartment storage values in MCS fen.

NEA (Network Environment Analysis) quantifies the relationships among compartments, environmental inputs and outputs. If two compartments are not directly connected, they can still affect one another through indirect connections involving other compartments. The analysis results are based on the final state of the simulation. The elements of the normalised flow matrix G_{ij} (Appendix) represent the quotient of the throughflow of j as a proportion of that received by i . The flow through $X5_{cat}$ is fully channelled into compartment $X1_{air}$ in both ecosystems. Dissolved carbon quotients $g61$ are 14.3 and 83.3 % in PSS bog and MCS fen, respectively. The percentage distribution of throughflow $X4_{acr}$ between $X1_{air}$, $X5_{cat}$ and $X6_{doc}$ in the studied PSS bog and MCS fen is the same and has a proportion 2.5 : 84.8 : 12.7 (%). EcoNet offers the calculation of many other quantitative estimates. In this article we consider only the most important indicators of the carbon status of forest-steppe mire ecosystems.

An important property of the mire ecosystem is the efficiency with which the main resource is used. The flow cycle index (FCI) is widely used in the context of ecological analysis of the functional state of ecosystems (Kazanci *et al.* 2009). It quantifies the proportion of throughflow due to the cyclic processes.

Both of the studied mire ecosystems were characterised by high FCI values (PSS bog 0.90, MCS fen 0.98). In a similar way, the share of total carbon reserve in the ecosystem, conditional upon cyclic processes, was assessed by the storage-based cycling index (SCI) (Ma & Kazanci 2014). High SCI values, as calculated by the model (PSS bog 0.90, MCS fen 0.98), were evidence of the 'maturity', as assessed by closeness to a steady state, of peat in sphagnum mires in the forest-steppe zone. A reutilisation measure (0.0 to 1.0) of carbon produced by decomposition and respiration for mires in the taiga zone was equal to 0.60 (Naumov 2004). It is highly likely that the high degree of internal closure of the biogeochemical carbon cycle of mire ecosystems is an adaptation mechanism to the extremely low concentration of carbon dioxide in the atmosphere everywhere.

Our previous studies have shown that the relationship between carbon cycle components, such as annual net primary production and soil respiration, is actually determined and controlled by the global mechanism supporting the biosphere (Naumov 2012, Naumov 2016). In this context, peat bogs occupy their specific place among the main types of terrestrial ecosystems.

Sensitivity analysis (SA)

In general, SA is necessary to assess the influence of the input measures of the model on the output of the state of the simulated object, i.e. to which input parameters the model is insensitive and to which it is most sensitive (Hamby 1994). In our study, sensitivity analysis was carried out to determine the key values that affect the reproduction of steady-state values of the X_i .

Variation of the photo-assimilation rate constant across a wide range of values did not affect the steady state of the X_i , except for the atmospheric carbon pool $X1_{air}$. The dependence of $X1_{air}$ on input parameter $k12$ had the form of a hyperbolic curve (Figure 5). Analysis of this showed that the maximum decrease in photo-assimilation rate will result in a fast accumulation of carbon dioxide in the ground layer of air. Under these conditions mire ecosystems easily turn into sources of CO_2 in the biosphere.

Negative linear dependence of S_i on $q1$ was established by means of varying values for each compartment. Reducing the value of input flow $q1$ increased the deviation from steady state values of carbon reserves in the compartments of the model. As expected, the least sensitive part of the ecosystem's total carbon pool was peat - the compartment containing by far the largest amount of carbon. Even in the total absence of carbon input from the atmosphere $S5$ did not exceed 1.8 % for MCS fen and 0.5 % for PSS bog. As for other compartments, S_i ranged from 12 to 17.5 % in MCS fen and from 11 to 13.5 % in PSS bog, which was no greater than measurement inaccuracy in carbon reserves in field experiments (Moore *et al.* 2002, Kosykh *et al.* 2008). High values of carbon cycling and small variation of steady state values in the absence of external sources allowed us to consider sphagnum peat mires in the forest-steppe zone as relatively autonomous natural phenomena.

Trial changes of input flow of dissolved carbon $q6$ in ecosystem MCS fen by 10 times (2 to 20 g m⁻² yr⁻¹) did not result in a significant shift of steady-state values $X1_{air}$ to $X5_{cat}$ ($S1$ to $S5 = \pm 7$ %). Maximum variation range of $S6$ was from +32 % to -40 %.

The shift of equilibrium reserve $X5_{cat}$ with change of the peat mineralisation rate constant $k51$ from 0.0001 to 0.001 yr⁻¹ was within ± 1 % for PSS bog and -1 to 1.7 % for MCS fen. The S_i indices of other compartments of PSS bog changed from 70 % at minimal values of $k51$ to -87 % at maximum values. For MCS fen the range of variation in $S1...S4$ was wider, from 70 to -112 %. The dissolved carbon pool at MCS fen was less sensitive to change in $k51$: the $S6$ index changed from 45 to -73 %.

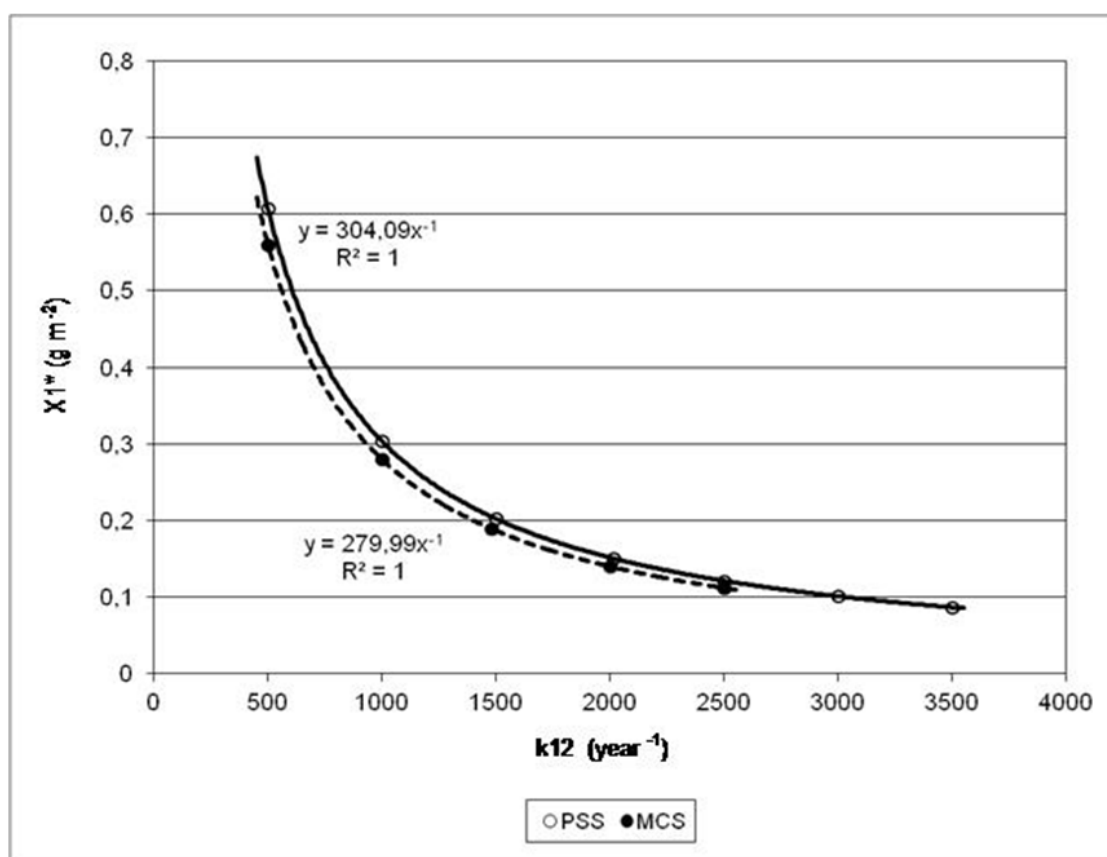


Figure 5. The dependence of $X1_{air}$ on input parameter $k12$.

Most sensitive to variation of constant values $k45$ of conversion of plant residues to peat within the range 0.05–0.35 were $X4_{acr}$ and $X6_{DOC}$. Their sensitivity index reached -266 % and -173 %, respectively, at low values of $k45$. At high values the shifts were 42 % and 27 %. The effects on other components of the system were weak and did not exceed ± 5.2 %. Peat was the least sensitive to variation of the input $k45$.

DISCUSSION

In the Introduction, we considered two approaches to modelling the carbon cycle processes in peatlands. In fact, these are two different aspects of a formalised description of carbon exchange in a peat-forming ecosystem. In the first approach, the task is to develop a mathematical model of the peat bog growth and the long-term accumulation of peat. In this direction, many interesting results were obtained, based both on historical data of peat accumulation in the Holocene period and on the inevitable simplifications and assumptions about the processes of peat formation, mineralisation of plant residues and peat, as well as on features of the hydrological regime.

The second aspect in modelling the carbon exchange of peatlands is based on system-wide features. The main task of this direction is to develop a dynamic model of the functioning of the carbon cycle of a peat bog as a natural ecosystem. To understand the functioning of the mire ecosystem as a whole, the second direction is preferable. Obviously, when modelling long-term peat accumulation without taking into account the many relationships between all parts of the ecosystem's carbon cycle in changing environmental conditions, it is impossible to obtain an adequate understanding of the process of carbon accumulation in peat and the carbon status of the mire ecosystem as a whole (Belyea & Baird 2006). These limitations stimulated the development of more complex models in the first direction (Belyea & Malmer 2004, Belyea & Baird 2006, Frohking *et al.* 2010, Heinemeyer *et al.* 2010, Morris *et al.* 2015, Waddington *et al.* 2015).

However, despite the increasing complexity of long-term peat accumulation models, they remain unsuitable for forecasting. The desire to take into account the influence of many external factors, direct and inverse relationships, often based on hypothetical functional dependencies, leads to a high sensitivity of simulation results to initial conditions such as the

nature of the microforms, the water-physical and reservoir properties of peat, the distribution of stocks of above-ground and underground biomass, net primary production, water balance, age of the bog, and the geometric shape of the peat deposit (Belyea & Clymo 2001, Belyea & Malmer 2004, Belyea & Baird 2006, Frolking *et al.* 2010, Heinemeyer *et al.* 2010).

In our opinion, ignoring the cyclic processes of carbon exchange in mire ecosystems and system-wide mechanisms of adaptation to changing external conditions significantly limit the value of developments in this area. The publication by Belyea & Baird (2006) is interesting in this context. The authors of the article, following Levin's (1998) essay, proposed to consider the peat bog as a 'complex adaptive system', CAS. Unfortunately, the article does not clearly define such important concepts as complexity and adaptability of peatlands. It is not clear to what extent the spatial and temporal boundaries of CAS should be considered in relation to the long-term peat accumulation process. Perhaps the authors are ahead of events, trying to anticipate the result. Following the internal logic of the cited publication, we find that peatland as CAS is a special system (not a generalised ecosystem) defined by a set of interconnected and interacting microforms. Patterns arise, develop and evolve under the influence of abiotic factors. The biotic component of the peat formation process remains outside the system altogether.

This mechanistic approach is not consistent with the ecological view of the problem. For example, it ignores biodiversity, trophic structure and biodiversity-productivity relationships, which are important features of an ecosystem as CAS (Levin 1998).

Adaptation and non-linearity

Adaptability is a characteristic property of living systems. Usually, adaptability is understood as a set of reactions of a living system that support its functional stability under changing environmental conditions (Reimers 1990). Belyea & Baird (2006) do not consider the stability of peatlands in modern conditions, and there are no clear definitions of the complexity and adaptability of the new expanding system. We consider the concept of CAS proposed by the authors of this publication to be premature.

The presence of nonlinear feedbacks and the nonlinear response of the system to external stimuli most likely indicate a significant deviation of the mire ecosystem from its steady state. It is generally true that, in most cases, the trajectory of a nonlinear system can be linearised in the vicinity of a stationary

state. We used this principle to study the properties of the stationary state of West Siberian mires. The balance of the carbon cycle processes is confirmed by the cycling indices FCI and SCI of peatlands that function in conditions of insufficient atmospheric precipitation.

A mire ecosystem is a complex of related components, united in time and space by multiple flows of matter and energy. Modelling helps the researcher to assess and analyse ecosystem properties that are not available for direct observations, to determine critical parameters of the state, and to develop most probable scenarios of the evolution of natural systems. Our model of the carbon cycle is applicable to mires of various types.

The raised bogs in the forest-steppe zone are of interest as model objects for estimating how the parameters of the carbon cycle vary. These forest-steppe bogs do not have sufficient resources for progressive growth to form significant massifs; they exist in the landscape as individual islands. Climate change, human activities and frequent fires are risk factors for examples of these unique natural objects situated on the southern edge of the area (Naumov *et al.* 2009).

Analysis of the mathematical model of the carbon cycle of sphagnum bog and mesotrophic fen revealed the existence of an asymptotically stable stationary solution in both cases. According to the scenario of development dynamics, a bog in the forest-steppe zone can reach a steady state after about 200 years under constant external conditions. Mesotrophic fen occupies a subordinate position in relation to raised bog. Its transition to equilibrium may take a longer time, and the carbon status and peat accumulation rate are controlled by the environment input q_6 .

Ecosystem analysis revealed a high degree of carbon cycling (FCI, SCI) in the mires. High values of cycling indices and small variation of steady-state parameters allow us to consider sphagnum peat bogs in the forest-steppe zone as relatively autonomous natural formations. The current carbon balance is largely determined by the physiological state of the primary producers. Limitation of photo-assimilation by external conditions or human intervention is a risk factor that can relatively easily turn a forest-steppe bog into a source of atmospheric CO₂.

We conclude that the northern peatlands, which have been accumulating carbon for millennia, continue functioning as a stabilising element in the global biogeochemical carbon cycle under modern conditions. A recent discussion (Alexandrov *et al.* 2020) raised the issue of limiting the carbon sequestration potential of peatlands and concluded that limiting carbon sequestration is highly likely in

the next fifty thousand years. However, it would be important to know what properties, internal connections and mechanisms can provide in this new state of mire ecosystems. Our calculations have shown that the mechanism of mire adaptation to low concentration of carbon dioxide in the atmosphere already now significantly limits carbon sequestration at the local level.

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Author for correspondence: Dr Aleksei Naumov, Laboratory of Biogeocoenology, Institute of Soil Science and Agrochemistry SB RAS, Lavrent'ev's Avenue 8/2, 630090, Novosibirsk, Russia.

E-mail: anaumov@issa-siberia.ru or aleksei_naumov@mail.ru



Appendix: the EcoNet 2.2 program and output

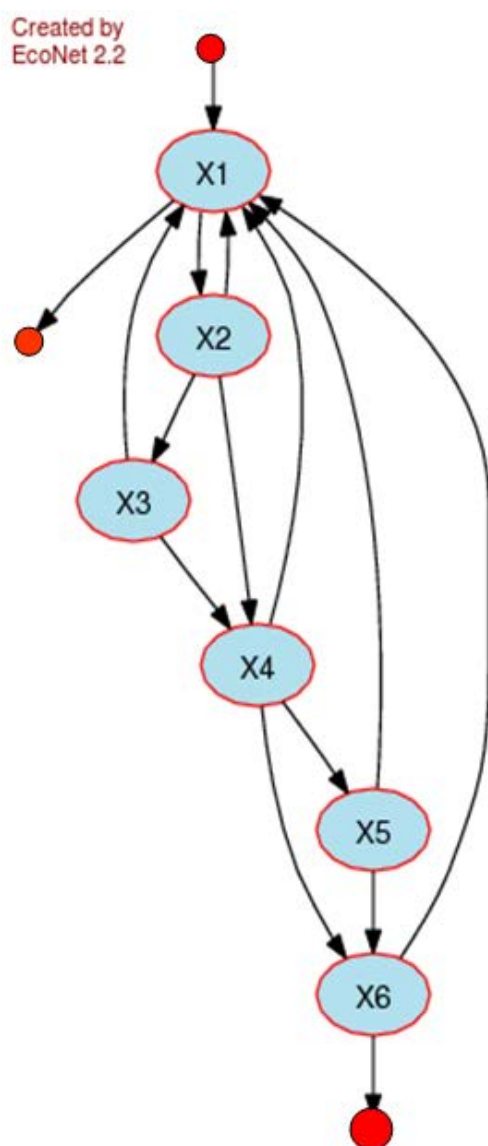


Figure A1. PSS bog network graph. The three red dots indicate external carbon flows in the mire ecosystem.

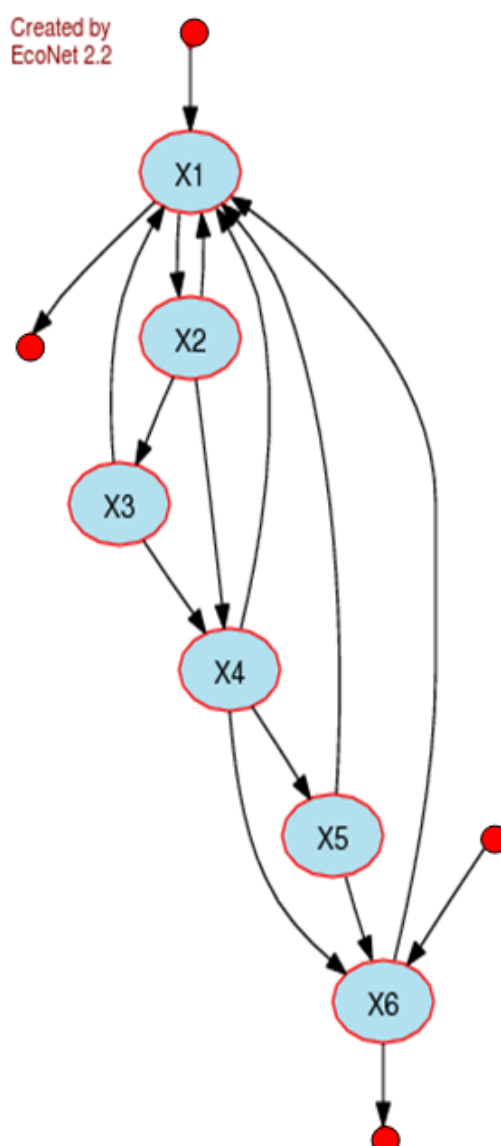


Figure A2. MCS fen network graph. The four red dots indicate external carbon flows in the mire ecosystem.

SIMULATION MODELLING OF THE CARBON CYCLE OF MIRE ECOSYSTEMS WITH THE ECONET 2.2 TOOLS

The following notation is used here and below:

X_n is the carbon pool of the compartment with the number n , as in Figure 1.

$X_n \rightarrow X_m$ denotes the process of carbon transfer from X_n to X_m and c is the rate constant of the corresponding process.

$(*) \rightarrow X_n$ and $X_n \rightarrow (*)$ denote the carbon exchange processes of the X_n compartment with the environment.

Dimension units as in Table 1.

1. Carbon cycle in raised sphagnum bog (simulation program)

* → X1	c=16	# atmospheric input flow
X1 → X2	c=2018	# photosynthetic assimilation
X2 → X3	c=0.57	# translocation of C into the roots
X2 → X4	c=0.15	# dying of above-ground shoots
X3 → X4	c=0.27	# dying of roots
X4 → X5	c=0.2	# peat formation
X5 → X6	c=0	# leaching of organic C
X6 → X1	c=0.01	# microbial degradation and gas evolution
X4 → X1	c=0.006	# destruction of dead mass
X3 → X1	c=0.3	# respiration of below-ground plant parts
X2 → X1	c=0.15	# respiration of above-ground phytomass
X5 → X1	c=0.0005	# peat mineralisation
X6 → *	c=0.06	# dissolved C output
X1 → *	c=0	# C gas output into the atmosphere
X4 → X6	c=0.03	# leaching of organic C

X1 = 0.16, X2 = 426, X3 = 1542, X4 = 2020, X5 = 246000, X6 = 240 # initial stock values:
 X1 - surface layer of atmosphere, X2 - above-ground phytomass, X3 - below-ground plant parts,
 X4 - dead plant residues, X5 - peat, X6 - dissolved C gases and organic matter.

Simulation results*Compartment properties*

Compartment	X1	X2	X3	X4	X5	X6
Initial storage C, g m ⁻²	0.16	426	1542	2020	246000	240
Final storage C (assumed steady-state), g m ⁻²	0.15	349	349	621	248400	266
Environmental input C, g m ⁻² year ⁻¹	16	0	0	0	0	0
Environmental output C, g m ⁻² year ⁻¹	0	0	0	0	0	16
Throughflow-in, g m ⁻² year ⁻¹	303.6	303.3	198.9	146.6	124.2	18.6
Throughflow-out, g m ⁻² year ⁻¹	303.3	303.6	198.9	146.6	124.2	18.6
Residence time, year	0.00050	1.15	1.75	4.24	2000	14.29
Trophic level	1	2	3	3.6	4.6	4.6

System-wide properties

Total system throughflow (TST) = 1095.2 g m⁻² year⁻¹

Flow cycling index (FCI) = 0.91

Storage cycling index (SCI) = 0.89

Flow matrix (**F**), g m⁻² year⁻¹:

	X1	X2	X3	X4	X5	X6
X1	0	52.3	104.7	3.7	124.2	2.7
X2	303.2	0	0	0	0	0
X3	0	198.9	0	0	0	0
X4	0	52.3	94.2	0	0	0
X5	0	0	0	124.2	0	0
X6	0	0	0	18.6	0	0

Normalised flow matrix (**G**):

	X1	X2	X3	X4	X5	X6
X1	0	0.172	0.526	0.025	1	0.143
X2	1	0	0	0	0	0
X3	0	0.655	0	0	0	0
X4	0	0.172	0.474	0	0	0
X5	0	0	0	0.847	0	0
X6	0	0	0	0.127	0	0

2. Carbon cycle in mesotrophic sedge-sphagnum fen (simulation program)

* → X1 c= 5 # atmospheric input flow
 X1 → X2 c= 1480 # photosynthetic assimilation
 X2 → X3 c= 0.72 # translocation of C into the roots
 X2 → X4 c= 0.23 # dying of above-ground shoots
 X3 → X4 c= 0.4 # dying of roots
 X4 → X5 c= 0.2 # peat formation
 X5 → X6 c= 0 # leaching of organic C
 X6 → X1 c= 0.1 # microbial degradation and gas evolution
 X4 → X1 c=0.006 # destruction of dead mass
 X3 → X1 c= 0.3 # respiration of below-ground plant parts
 X2 → X1 c= 0.3 # respiration of above-ground phytomass
 X5 → X1 c= 0.001 # peat mineralisation
 X6 → * c= 0.02 # dissolved C output
 X1 → * c= 0 # C gas output into the atmosphere
 X4 → X6 c= 0.03 # leaching of organic C
 * → X6 c= 5 # dissolved C input

X1 = 0.16, X2 = 343, X3 = 1795, X4 = 2300, X5 = 90750, X6 = 200 # initial stock values:
 X1 - surface layer of atmosphere, X2 - above-ground phytomass, X3 - below-ground plant parts,
 X4 - dead plant residues, X5 - peat, X6 - dissolved C gases and organic matter.

Simulation results

Compartment properties

Compartment	X1	X2	X3	X4	X5	X6
Initial storage C, g m ⁻²	0.16	343	1795	2300	90750	200
Final storage C(assumed steady-state), g m ⁻²	0.16	187.9	193.3	510.6	95561	169.2
Environmental input C, g m ⁻² year ⁻¹	5	0	0	0	0	5
Environmental output C, g m ⁻² year ⁻¹	0	0	0	0	0	3.4
Throughflow-in, g m ⁻² year ⁻¹	234.9	234.9	135.3	120.5	102.1	20.3
Throughflow-out, g m ⁻² year ⁻¹	234.9	234.9	135.3	120.5	95.6	20.3
Residence time, year	0.00068	0.80	1.43	4.24	1000	8.33
Trophic level	1	2	3	3.6	4.9	1

System-wide properties

Total system throughflow (TST) = 841.4 g m⁻² year⁻¹
 Flow cycling index (FCI) = 0.98
 Storage cycling index (SCI) = 0.98

Flow matrix (**F**), g m⁻² year⁻¹:

	X1	X2	X3	X4	X5	X6
X1	0	56.37	57.98	3.06	95.56	16.92
X2	234.90	0	0	0	0	0
X3	0	135.30	0	0	0	0
X4	0	43.22	77.31	0	0	0
X5	0	0	0	102.11	0	0
X6	0	0	0	15.32	0	0

Normalised flow matrix (**G**):

	X1	X2	X3	X4	X5	X6
X1	0	0.240	0.429	0.0254	1	0.833
X2	1	0	0	0	0	0
X3	0	0.576	0	0	0	0
X4	0	0.184	0.571	0	0	0
X5	0	0	0	0.847	0	0
X6	0	0	0	0.127	0	0