

An empirical model of carbon fluxes in Russian tundra

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Abstract

This study presents an empirical model based on a GIS approach, which was constructed to estimate the large-scale carbon fluxes over the entire Russian tundra zone. The model has four main blocks: (i) the computer map of tundra landscapes; (ii) data base of long-term weather records; (iii) the submodel of phytomass seasonal dynamics; and (iv) the submodel of carbon fluxes. The model uses exclusively original *in situ* diurnal CO₂ flux chamber measurements (423 sample plots) conducted during six field seasons (1993–98). The research sites represent the main tundra biome landscapes (arctic, typical, south shrub and mountain tundras) in the latitudinal diapason of 65–74°N and longitudinal profile of 63°E–172°W. The greatest possible diversity of major ecosystem types within the different landscapes was investigated. The majority of the phytomass data used was obtained from the same sample plots. The submodel of carbon fluxes has two dependent [GPP, Gross Respiration (GR)] and several input variables (air temperature, PAR, aboveground phytomass components). The model demonstrates a good correspondence with other independent regional and biome estimates and carbon flux seasonal patterns. The annual GPP of Russian tundra zone for the area of 235×10^6 ha was estimated as $-485.8 \pm 34.6 \times 10^6$ tC, GR as $+474.2 \pm 35.0 \times 10^6$ tC, and NF as $-11.6 \pm 40.8 \times 10^6$ tC, which possibly corresponds to an equilibrium state of carbon balance during the climatic period studied (the first half of the 20th century). The results advocate that simple regression-based models are useful for extrapolating carbon fluxes from small to large spatial scales.

Keywords: arctic ecosystems, CO₂ flux chamber measurements, carbon balance, global climate change, modelling, Russia

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Introduction

The problems arising from the warming effect of global climate change lead stress the need for improved estimates of the main components of the carbon cycle at the macro-regional scale. Although recent studies in Alaskan tundra have contributed widely to a better understanding of arctic carbon fluxes and stocks and many new field programs in the North America have been undertaken (ARCSS/LAII Flux Study 1998), only a few intensive studies on carbon fluxes had been made in the Russian arctic during the nineties. Many valuable data on arctic soil respiration in Cherski region (North Yakutia) were obtained and analysed by Zimov *et al.* (1996) and Fedorov-Davydov (1998). Sommerkorn (1998)

put special emphasis on those factors controlling soil respiration and moss photosynthesis in major tundra types of Eastern Taimyr Peninsula. Extensive research into environmental controls on soil respiration was undertaken by Christensen *et al.* (1998) along the Russian arctic coast. Nevertheless, it is clear that there is still a big gap in our knowledge of circumpolar processes because of the paucity of whole-ecosystem field studies of carbon balance in Russian tundra, which represents about 32% of the surface area of Russia (Karelin *et al.* 1994).

In this paper, we aimed to establish full-scale characteristics of biogenic macro-fluxes of carbon over the entire Russian tundra zone. The principal idea was to construct a simple yet adequate, empirically based model for large-scale estimates of carbon fluxes, that can also run at a single site. With this aim in mind, regression-

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based models of carbon fluxes and GIS-approach were chosen as tools. Our original *in situ* CO₂ exchange and attendant measurements from whole ecosystems in different Russian tundra regions served as an empirical base for the modelling.

Use of a regression-based approach

From the methodological point of view there are two extreme types of simulation models, namely the empirical (e.g. phenomenological, regression-based, statistical or correlative) and process-based (e.g. mechanistic or dynamic), with a wide range of transitional variants in-between. Models of the first type approximate a complex variable like gross primary productivity or respiration as a function of significant ecological factors, within the error term of approximation (Gilmanov 1996). In this case the classic methods of regression analysis are applicable. The advantages of the regression-based approach in handling and analysis of empirical information have been demonstrated repeatedly by investigators of productivity in arctic ecosystems, especially when applied to spatial estimates (Lieth 1975; Wielgolaski *et al.* 1981; Esser 1991; Gilmanov 1996). Various methods of regression modelling were widely applied to the IBP data treatment in the seventies and eighties (Bliss *et al.* 1981) and are still in use in current studies on the respiration of tundra ecosystems (e.g. Sommerkorn 1998 and Christensen *et al.* 1998). (Amongst continuing projects in this field of interest, note the spatial phenomenological model 'Regional Approach for CO₂ flux Integration and Extrapolation (RACIE)' by G.L. Vourlitis and W.C. Oechel.)

Unlike regression modelling, process-based models use our detailed knowledge of latent natural mechanisms, usually expressed as a system of difference or differential equations, which simulate the temporal changes in ecosystem output variables. This approach is rightly considered an effective instrument of ecosystem analysis (Leuning *et al.* 1995; Gilmanov 1996). Amongst the successful examples of this type are grassland, forest and general ecosystem models (e.g. SENTURY, GEM, TEM and TBM) but, until recently, equivalent models for arctic ecosystems (e.g. Bunnell & Scoullar 1975; Reynolds & Leadley 1992; Waelbroeck 1993) were less developed. While, recent advances in arctic modelling inspire much optimism for significant improvement, existing process-based models are not suitable for global and regional estimates, especially of ecosystem productivity or biogeochemical cycles. This is mostly a consequence of the large number of parameters required, which widely vary at temporal and spatial scales and are unknown for the majority of ecosystems (Leuning *et al.* 1995). The growing complexity of process-

based models results in the increase of uncertainties by accumulation of parameter errors. The extrapolation to macro-scale needs simple models that are parameterized easily (Leuning *et al.* 1995). Regression-based models are thus very useful here, especially if a rapid spatial estimates based on readily available empirical data are needed. This approach ignores the mechanisms of the process itself in favour of a definite set of readily defined macro-controls. Because of this, regression-based modelling might also be used for independent testing of process-based models or as a base for their construction.

Materials and methods

Overview

The present study is a further generalization of our earlier results, including the construction of databases and computer maps (Karelin *et al.* 1994; Zamolodchikov *et al.* 1995), the analysis of CO₂ flux measurements (Zamolodchikov *et al.* 1998, 2000), and modelling of carbon fluxes in tundras (Zamolodchikov *et al.* 1997; Zamolodchikov & Karelin 1999). Estimates of the carbon balance of Russian tundras were calculated using seasonal and geographical extrapolations based on regression modelling.

In this section we enlarge upon terms used for ecosystem/landscape classification, field sites and methods of measurements, model development, testing and application. Note that the model was verified using our new unpublished field data obtained in 1998–99.

Ecosystem and landscape classification

Before proceeding further, it is necessary to establish our terms for ecosystem/landscape classification. We consider herein the Russian tundra to be a biome or zone as a consequence of its large area and continuous latitudinal distribution. The Russian tundra biome is subdivided into tundra and forest tundra geographical landscapes. The forest tundras are beyond our consideration here because of the lack of original field CO₂-exchange measurements in these landscapes. Amongst tundra landscapes we modelled only the landscapes within the boundaries of zonal/latitudinal tundra distribution in Russia. There are six zonal landscapes: polar deserts, arctic, typical and south tundras, mountain polar deserts, and mountain tundras. There are also two azonal landscapes: bogs and river valleys. Bogs and river valleys form new landscapes within the above-mentioned types, where presented. We consider here only those mountain tundras and mountain polar deserts located within the limits of zonal distribution of Russian tundra biome (Fig. 1). For instance, mountain tundras within a forest

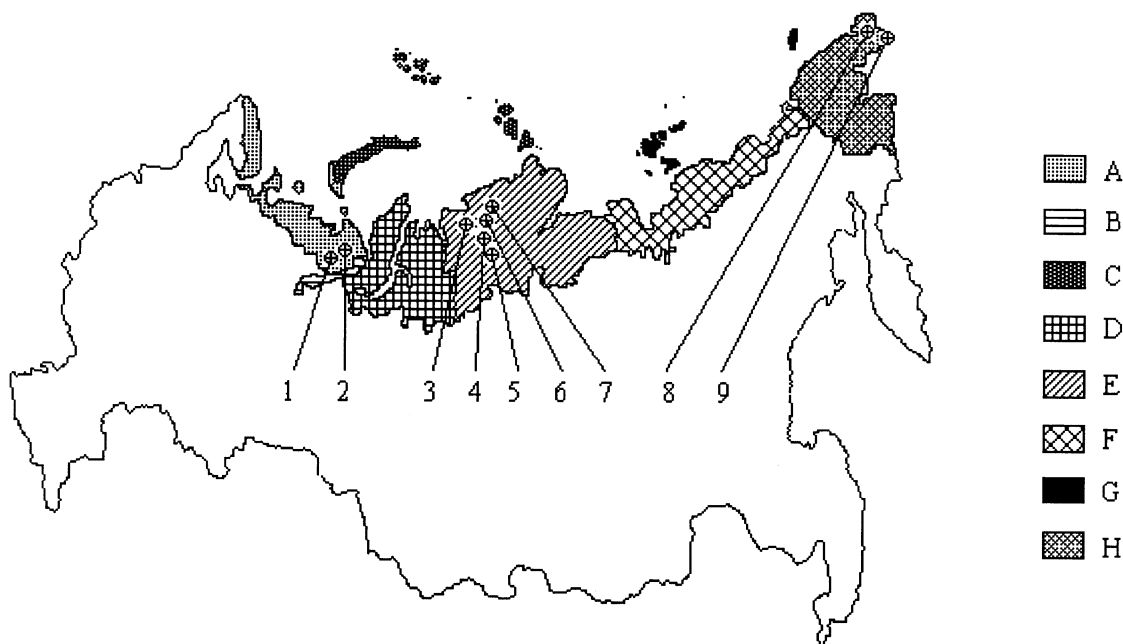


Fig. 1 The schematic map of Russian tundra regions: A, East-European region; B, Polar Ural; C, Western islands of Russian Arctic; D, West Siberia; E, Central Siberia; F, Yakutiya; G, Eastern islands of Russian Arctic; H, Chukchi-Anadyr region. Site locations: 1, Talnik; 2, Khalmer-U; 3, Pura; 4, Agapa; 5, Kresti; 6, Tareya; 7, Aya-Turku; 8, Ioni; 9, Chaplino (see text for details)

zone were not taken into consideration. Fifteen different geographical tundra landscapes were identified over the Russian tundra zone, not including bogs and river valleys in polar deserts and bogs in mountain polar deserts missing in the landscape map used.

In the present paper the entire area of Russian tundra zone was also subdivided into eight geographical regions/provinces from East European tundra in the West to the Chukchi-Anadyr province in the East (Fig. 1). This is convenient in terms of further comparison between independent regional estimates to be found in Russian literature, and the corresponding values calculated by our model. Any given region has a certain number of the tundra landscape types listed above. Thus, the Western Islands region of the Russian arctic represents only polar deserts and arctic tundra (i.e. two landscapes). The Central Siberia region has mountain tundra, mountain tundra bogs, mountain tundra river valleys, typical tundra, typical tundra river valleys, etc., giving a total of 13 types of different geographical landscapes that we would call 'regional landscapes'. The overall number of these regional landscapes in Russian tundra is 69.

Field sites and methods

Data on C-CO₂ fluxes and their environmental controls were collected during six field seasons in 1993–98 (Zamolodchikov *et al.* 1997, 1998; Zamolodchikov &

Karelin 1999) at nine different locations (Fig. 1): in the East European tundras [Talnik (1996: 67°20'N, 63°44'E), Khalmer-U (1995: 67°57'N, 64°40'E)], in Central Siberia [West of the Taymyr Peninsula: Kresti (1993–94: 70°51'N, 89°54'E), Agapa former IBP site (1993: 71°26'N, 89°14'E), Pura (1993: 72°17'N, 85°45'E), Tareya former IBP site (1993–94: 73°15'N, 90°36'E), Aya-Turku (1994: 73°56'N, 91°54'E)] and in the Chukchi-Anadyr tundra region [East of the Chukotskiy Peninsula: Chaplino (1997: 64°26'N, 172°30'W), Ioni (1998: 65°48'N, 173°22'W)].

Overall we studied 29 different tundra ecosystems/sites in nine landscapes. The research sites represent the main geographical landscapes within the Russian tundra biome in the latitudinal diapason of 65–74°N and longitudinal profile of 63°E–172°W. More than 50% of the diversity of ecosystem types within the tundra landscapes was investigated. They represent about 70% of all tundra ecosystems by area and more than 90% by C storage.

Our field studies in different years were conducted during periods of snow melt, active plant growth and formation of constant snow cover. The estimation of diurnal C-CO₂ fluxes by means of the closed gas-exchange system was the main component of our field research. Changes in CO₂ concentrations were measured using a portable infrared gas analyser (LiCor-6200, Nebraska, USA; for details of the sampling system and measuring technique see Vourlitis *et al.* 1993). During each measurement of CO₂ fluxes, a transparent chamber

for photosynthetically active radiation (PAR) was placed and sealed onto permanent square sample plots of 40×40 cm. In order to prevent air leakage between chamber and environment we used stainless steel or aluminium square frames inserted 15 cm deep into the soil with water locks. The height of the chambers varied from 25 to 60 cm depending on the vegetation. The flux values were calculated from chamber rates of CO_2 concentration which increase or decrease during exposure (c. 1 min). It was assumed that the flux values under natural solar radiation were estimates of net ecosystem carbon flux (NF), while those in the darkened chamber were estimates of gross ecosystem respiration (GR). The difference between these parameters is the gross primary production (GPP). We arbitrarily accepted the GPP flux to be negative (carbon accumulation) and GR flux (carbon loss to the atmosphere) to be positive, following the conventional practice (Oechel *et al.* 1993; Waring *et al.* 1995). Net flux (NF) and respiration measurements were conducted over 24-h periods every 5–10 d in all studied ecosystems. During each diurnal measurement, plots were measured every 1.5–2 h. As a result, a diurnal dataset for each sample plot included 15–20 instant carbon flux values, which thereafter served for the linear approximation of intradiurnal dynamics of fluxes and calculation of the integrated diurnal values. The overall dataset includes 423 diurnal estimates of GPP, GR and NF from 127 permanent sample plots.

In addition, chamber temperature and relative humidity, and ambient PAR were recorded (LiCor-6200 sensors). Temperature of ambient air and soil temperatures at 0, 1, 5 and 10 cm below the surface were monitored using type-T thermocouples. Depth of thaw at each site was determined using a steel rod inserted through the unfrozen soil at 20 random points, when flux measurements at a particular site were complete. Soil moisture in the top 5 cm was measured gravimetrically after completion of regular diurnal measurements at each site.

At all sample plots after each diurnal measurement the relative projective cover of different plant forms was also determined. At the end of each field season the above-ground phytomass of vascular plants, mosses and lichens was cut, sorted by components, oven-dried and weighed for all sample plots. During the season the dynamics of phytomass were estimated indirectly using our regression equations for the aboveground components of phytomass vs. their partial vegetative cover (Zamolodchikov *et al.* 1997).

Model development

The regression-based model of carbon fluxes was approximated by results of our CO_2 exchange and other

environmental and plant biomass measurements. The flux simulation patterns differed significantly for the 'warm' (mean long-term diurnal air temperature is $\geq 0^\circ\text{C}$) and 'cold' ($< 0^\circ\text{C}$) parts of a season. The model for the 'warm' period was based on the results of our own field investigations. The source data were grouped into a matrix, which includes 423 rows (i.e. the total number of diurnal measurements of sample plots). The matrix columns are the appropriate values of carbon fluxes (NF, GR, GPP), phytomass sample characteristics, and averaged diurnal weather records. We should note here that our source data included further environmental controls, like depth of active layer, soil temperatures and moisture, water table, wind speed, etc. that were not used in further modelling (for reasons see 'Discussion' below).

The preliminary analysis revealed a significant correlation between carbon fluxes as dependent variables and air temperature, PAR, and phytomass of vascular plants as independent variables (Fig. 2). To approximate these relationships we used linear equations instead of the nonlinear functions commonly used for this purpose. Amongst others, an asymptotic function was proposed to formalize the relationship between PAR and production (Monsi & Saeki 1953), and the exponential function for the relationship between temperature and respiration (Ryan 1991). But the use of nonlinear expressions in our case didn't improve the accuracy of the model significantly and therefore we chose the more simple linear form of equations. The parameters were estimated using the procedures of a step-wise multiple regression analysis at a significance level of 0.1. This resulted in the following equations for gross primary production (GPP: $\text{gC m}^{-2} \text{d}^{-1}$) and gross ecosystem respiration (GR: $\text{gC m}^{-2} \text{d}^{-1}$):

$$\text{GPP} = 0.9 - 0.099 \cdot \text{PAR} - 0.086 \cdot T_a - 0.0452 \cdot \text{GS} - 0.0207 \cdot \text{GG} - 0.00361 \cdot \text{WDS} - 0.00179 \cdot \text{M}, \quad (1)$$

$$(n = 423, R^2 = 0.670, \text{SE} = 1.0597)$$

$$\begin{aligned} \text{GR} = & -0.57 + 0.029 \cdot \text{PAR} + 0.164 \cdot T_a + 0.0205 \cdot \text{GS} + \\ & 0.0049 \cdot \text{GDS} + 0.0091 \cdot \text{GG} + 0.00117 \cdot \text{WS} + \\ & 0.00335 \cdot \text{WDS} + 0.00146 \cdot \text{M} - 0.00076 \cdot L, \end{aligned} \quad (2)$$

$$(n = 423, R^2 = 0.753, \text{SE} = 0.7526)$$

where PAR is a diurnal sum of photosynthetically active radiation ($\text{MJ m}^{-2} \text{d}^{-1}$), T_a is mean diurnal air temperature ($^\circ\text{C}$), GS is the mass of foliage of shrubs (here and below in grams of oven-dried weight), GDS is the mass of foliage of dwarf shrubs, GG is the above-ground living mass of grasses, WS is the above-ground mass of shrub woody components, WDS is the above-

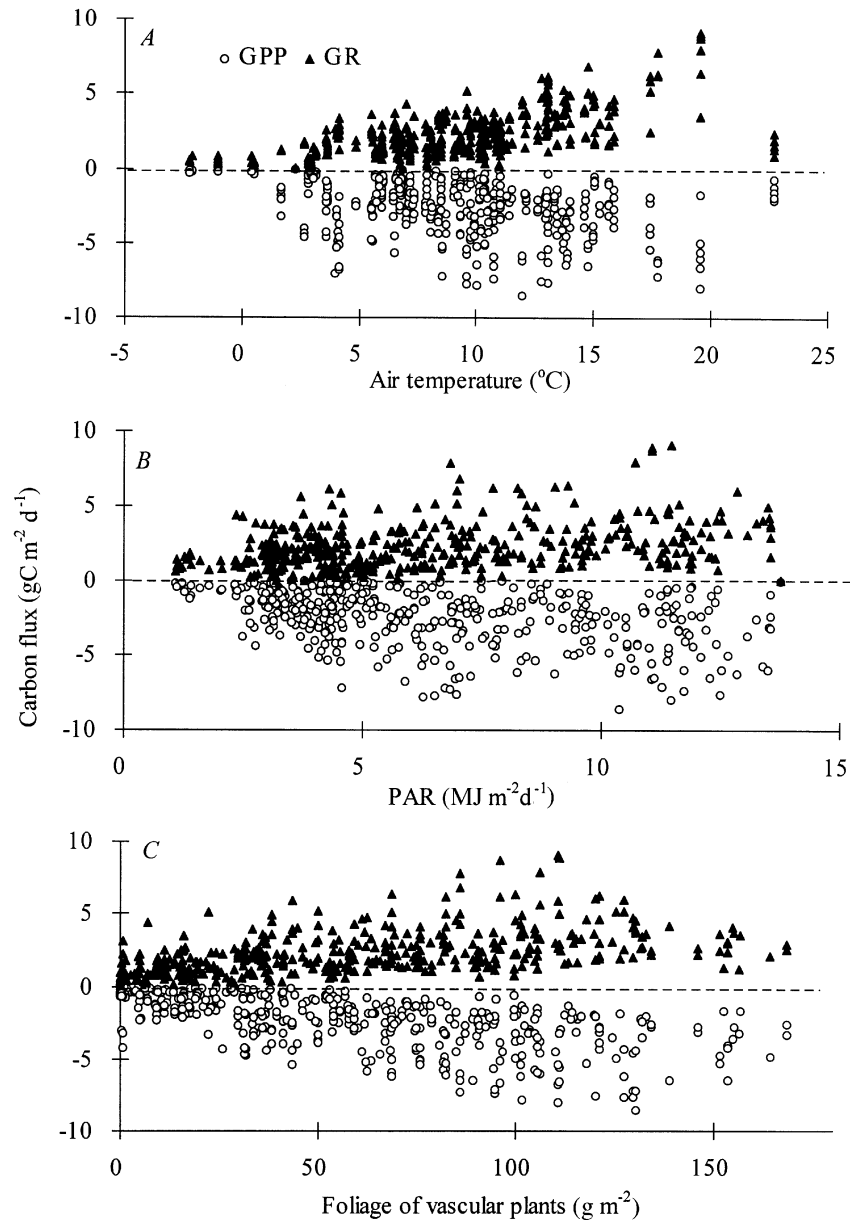


Fig. 2 The diurnal values of gross primary production (GPP) and gross respiration (GR) vs. diurnal average air temperature (a), diurnal sum of PAR (b) and mass of foliage of vascular plants (c) in Russian tundras

ground mass of dwarf shrub woody components, M is the living phytomass of mosses, and L is the living phytomass of lichens.

The above-mentioned equations allow us to predict the values of diurnal carbon fluxes during the warm period of the year using the data on PAR, air temperature and phytomass of growth forms and their components with appropriate accuracy. Notice that approximations of the source datasets (Fig. 3) are prevented from considerable systematic errors in the areas of big values of production and respiration, where one might expect a manifestation of nonlinear effects. The observed scatter in the data is mostly random or a consequence of the possible influence of other controls not included into analysis.

It is well known that the processes of carbon exchange take place not only in warm period of the year, but also in winter. Surveys in Alaska and the Kolyma lowlands have also shown that CO_2 emission in tundra and forest tundra zones might occur from even the totally frozen active soil layer (Fedorov-Davydov & Gilichinskii 1993; Zimov *et al.* 1996; Oechel *et al.* 1997). We collected available data from the literature on the values of winter carbon emission, including our own measurements during the periods of snow melt (North-Eastern European shrub tundra) and the beginning of snow cover formation (North-Western Taymyr) (Fig. 4). These data were formalized in the form of the following equation for winter emission (WE , $\text{gC m}^{-2} \text{d}^{-1}$):

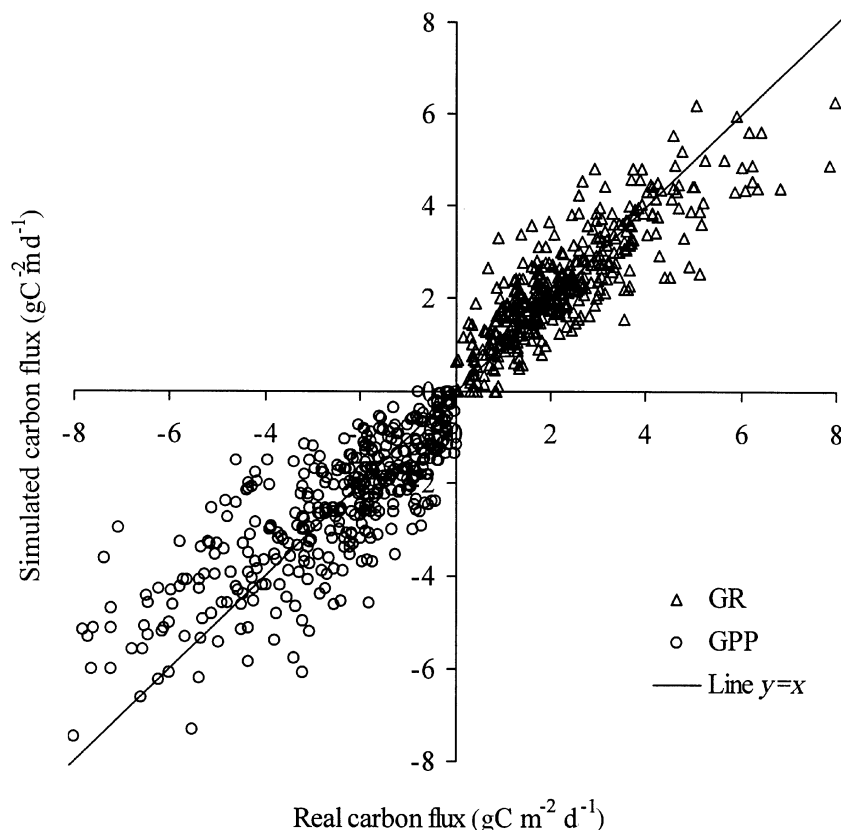


Fig. 3 Modelled vs. measured values of gross primary production (GPP) and gross respiration (GR) including line $y=x$.

$$WE = 0.639851 - 0.00893 \cdot NOR + 0.002247 \cdot (WD - 18)^2, \quad (3) \\ (n = 37, R^2 = 0.6399);$$

where *NOR* is geographical latitude (degrees North), and *WD* is a number of a time step starting with the beginning of September. This equation was used to estimate the values of winter emission in arctic, mountain, typical and south shrub tundras. Unfortunately, we were unable to calculate the above estimates for polar deserts because of the lack of specific source information for Russian regions.

Model testing

We tested the regression-based submodel of carbon fluxes on independent empirical CO_2 -flux, plant biomass and weather datasets obtained in the shrub tundra at Talnik field site from 26 June to 12 August 1999. Carbon emission data from the same site during the cold season of 1998–99 were also used.

As an example we will focus on seasonal flux changes in the dwarf-shrub community. The results of the modelling are in good agreement with field data on summer carbon fluxes (Fig. 5). There were significant correlations between measured and predicted fluxes ($R = 0.86$ (NF), 0.86 (GR) and 0.87 (GPP), $P < 0.05$). The

empirical values of NF, GR and GPP, integrated over the length of field season (84 days), constituted 37.3 ± 10.6 , 176.4 ± 25.0 , $-139.1 \pm 26.3 \text{ gC m}^{-2} \text{ seas}^{-1}$, respectively. The corresponding modelled values (24.4 ± 9.3 , 167.2 ± 22.8 , $-142.8 \pm 26.7 \text{ gC m}^{-2} \text{ seas}^{-1}$) are within the limits of standard errors for the field estimates. The differences between the corresponding means are insignificant (paired *T*-test, $P = 0.45 \div 0.73$).

Equation (3) approximates winter carbon emissions on only a limited dataset and hence it needs rigorous testing. Figure 6 demonstrates the seasonal dynamics of carbon emissions based on measurements and modelling. Notice the good correspondence between most empirical and modelled values, except the end of September and the beginning of December, results of the considerable scatter of the source data for this period (Fig. 4). The correlation between the empirical and approximated values is significant ($R = 0.96$, $P < 0.05$). The mean winter efflux ($0.17 \text{ gC m}^{-2} \text{ d}^{-1}$) is not significantly different from the model estimate ($0.19 \text{ gC m}^{-2} \text{ d}^{-1}$; paired *T*-test, $P = 0.70$).

Model application

The application of the model to the spatial and intra-annual simulation of carbon fluxes in the Russian tundra

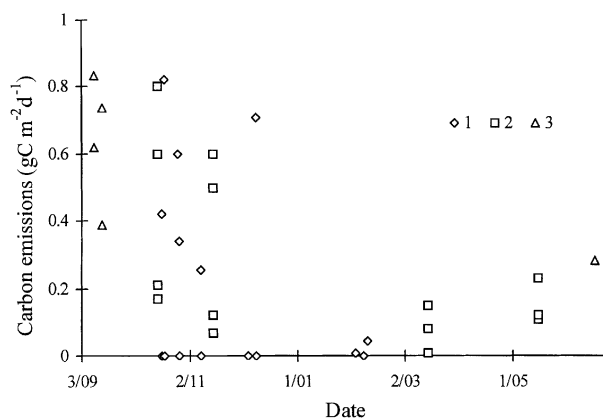


Fig. 4 Carbon emission in tundras during the winter period. 1, data of Fedorov-Davydov & Gilichinskii (1993); 2, data of Oechel *et al.* (1997); 3, the present study

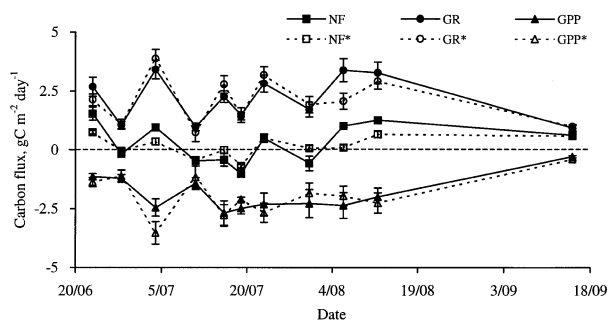


Fig. 5 Field measurements of C-CO₂ net flux (NF), gross primary production (GPP) and gross respiration (GR) in south shrub tundra near Talnik site during the warm period of 1999, and regression modelling. Data are averages $\pm$ SE, $n=4$ sample plots. (*), model approximations

zone followed the main principles of geo-information systems (GIS). Source data for GIS-modelling included (i) a computer map of tundra landscapes, (ii) a macro-meteorological database, and (iii) the submodel of seasonal phytomass changes.

(i) The computer map of tundra landscapes was derived from the landscape map of the former Soviet Union at the scale of 1:4 000 000 (Isachenko *et al.* 1988). We had used this previously for the estimation of carbon stocks in phytomass and primary production of the Russian tundra zone (Karelin *et al.* 1994; Zamolodchikov *et al.* 1995). The computer map includes the boundaries of tundra biome geographical landscapes and eight geographical regions.

(ii) The macro-meteorological database describes the dynamics of diurnal means of air temperature and diurnal sums of PAR in all regional landscapes using 36 intra-annual time steps. These values were calculated using the long-term meteorological records from 135 weather stations over the Russian tundra biome. For individual regional landscapes the weather data were

averaged by all weather stations found on its territory. Because the available source information (Weather data records of the USSR 1966–68) was presented by monthly means, which is too coarse for modelling carbon fluxes during a 'warm' season, the monthly means of air temperatures and PAR were recalculated onto 36 intra-annual time steps using cubic spline-interpolation.

(iii) The submodel of aboveground phytomass changes reconstructs the landscape dynamics of the aboveground components of living phytomass during the warm season with the same time step. These components are the woody and green parts of shrubs and dwarf shrubs, grasses, mosses and lichens. The source information was collected in a database including 145 different local tundra ecosystems from more than 40 literary sources (see full list of References in: Bazilevitch 1993) and 19 originally sampled ecosystem types including the overall data on 165 phytomass sample plots.

Because most of these sources provided only the information on seasonal maxima of phytomass storage, we simulated the continuous dynamics of the green components of phytomass using a symmetrical sinusoidal function. The phytomass values of woody components, mosses and lichens were arbitrarily accepted to be invariable.

It is self-evident that the results of modelling might be affected considerably by the source data we used. Periods of meteorological observation in the weather stations (Weather data records of the USSR 1966–68) differed considerably, but in general the observation period for air temperatures was estimated as 1900–60 and for solar radiation 1945–60. The phytomass dataset is much more recent: almost all published data were obtained in 1965–80 (approx. IBP period), and constitutes 50% of all the phytomass data that we used. The remaining 50% is from our original recent estimates (1993–98).

Therefore, our source data on climate and phytomass reserves do not cover the 1980s and 1990s, i.e. the most important period in terms of global warming¹. It is more likely that the climatic period that we observed in this study is more consistent with a balanced, near-equilibrium, climax state of tundra ecosystems in Russia.

Finally, we reconstructed changes of meteorological factors and phytomass components in all 69 regional landscapes of Russian tundra biome for 36 intra-annual time steps. These data were incorporated into calculations of carbon fluxes in these landscapes during the warm period using (1) and (2). During the cold period the fluxes were estimated using (3), the average geographical latitudes of the computer map regional

¹ The reason we didn't use the more recent climate records (1961–97) for modelling resulted from cost limitation for weather data from the State Meteorological Center (Obninsk, Russia).

landscapes and the numbers of time-step intervals starting with the beginning of September. This resulted in a matrix of carbon flux means by all 69 regional landscapes on every time-step. Because the modelling was based on a whole (365-day) year, we used variable lengths of time-steps (for instance, in August there are 3 time-steps of 10, 10 and 11 days). The total annual estimates were integrated by seasonal data assuming that flux changes between time-steps were linear. The appropriate sums of these values give us spatial estimates of carbon fluxes over the entire Russian tundra zone.

The standard errors for the model estimates were calculated using the source standard errors (SE) of carbon diurnal fluxes from (1) to (3). The integral seasonal and annual standard errors for individual landscapes (SE_{Li}) were the appropriate sums of values of diurnal standard errors (SE). The standard errors of regional C fluxes values were estimated as: $SE_R = \sum_{i=1,n} (SE_{Li}) / \sqrt{n}$, where n is the total number of landscapes in a geographical region, SE_{Li} is the standard error of the i th geographical landscape C flux. To calculate the standard error of C fluxes for the entire Russian tundra zone, the same formula was used with standard errors of regional tundra landscapes and their total number as n ($n=69$).

Results

Seasonal dynamics of carbon fluxes

Figure 7 shows the generalized dynamics of simulated fluxes in Russian tundra landscapes during the warm season. All curves look relatively smooth mainly as a consequence of the long-term nature of the source meteorological data used. But it should be borne in mind that any significant weather fluctuations may cause considerable changes in carbon fluxes (Oechel *et al.* 1995; Zamolodchikov *et al.* 1997, 1998).

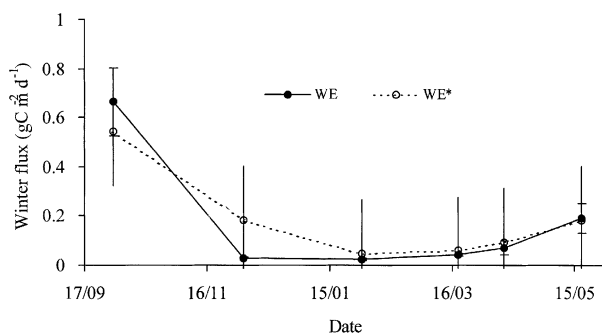


Fig. 6 Dynamics of winter C-CO₂ efflux (WE) in south shrub tundra during the cold period of 1998–99 (Talnik site). (*), model approximations

The seasonal dynamics of the integrated signal of C-CO₂ efflux is of special interest, as it determines changes in CO₂ concentration in the atmosphere above if mixing is neglected. It can be seen (Fig. 8) that the maximum of the integrated flux falls in May, i.e. the period when maximum amount of carbon dioxide is emitted to the atmosphere, whereas the minimum, marking the greatest rate of CO₂ absorption, falls in September. Both extreme points are in good agreement with atmospheric changes of CO₂ in arctic latitudes. An example is found in 1996 seasonal records of CO₂ concentrations from CMDL at Barrow, Alaska (Hofmann *et al.* 1998). Although this region is situated in North America, it matches the modelled area with respect to its latitudinal and biome location. Figure 8 shows that in 1996 the maximum and minimum of atmospheric CO₂ concentrations at Barrow also fall in May and September, respectively. In 1997 the positions of the seasonal extremes were in April and August. The modelled integrated flux and atmospheric CO₂ concentration were correlated at 0.95 for 1996 and 0.91 for 1997 ($P < 0.05$).

The model is consistent with major empirical patterns of seasonal changes in net carbon flux. The end of snow

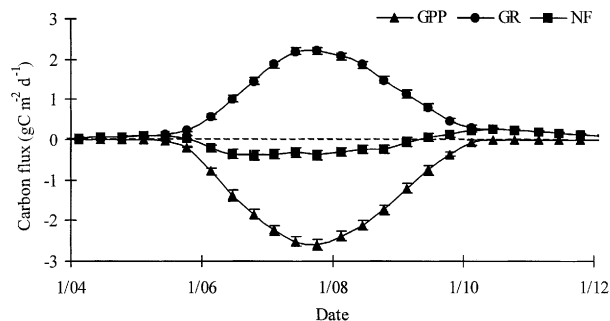


Fig. 7 The general dynamics of carbon fluxes in Russian tundras in April–November using the model presented in this paper. For abbreviations see Figs 2,3

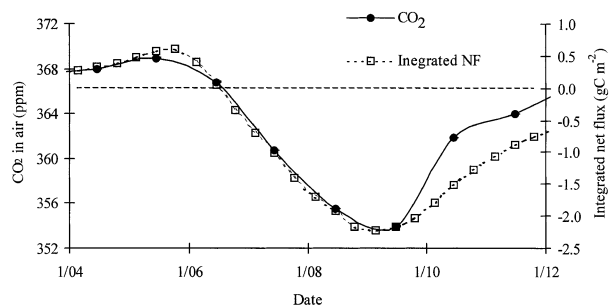


Fig. 8 Integrated carbon net flux (NF) in Russian tundra zone (using the present model) and 1996 changes in atmospheric CO₂ concentration in Barrow, Alaska (using CMDL data; see Hofmann *et al.* 1998).

melt in the model was demonstrated to coincide with a period of spring emission of carbon dioxide (Fig. 9), as normally occurs *in situ* (Oechel *et al.* 1995; Zamolodchikov *et al.* 1998). Later, in the middle of the growing season, tundra communities act mostly as a carbon sink. At the end of the warm season the carbon balance changes its pattern from sink to source (the so-called period of 'autumnal carbon emission'). Compared with spring, the modelled autumnal emission has a much higher rate (Fig. 9), as has also been shown in many other studies (e.g. Oechel *et al.* 1995; Zamolodchikov *et al.* 1997).

According to the model, during the warm period (117 days) of the 365-d 'long-term' year the average rate of GPP in Russian tundras is -1.77 , whereas GR is $+1.52$, with NF of $-0.24 \text{ gC m}^{-2} \text{ d}^{-1}$. The average rate of winter emission ('cold period': 248 days) is $+0.094 \text{ gC m}^{-2} \text{ d}^{-1}$.

Spatial variation of annual fluxes

The integration of seasonal dynamics allows us to calculate the annual rates of carbon fluxes in all 69 regional landscapes. The sum of these values cor-

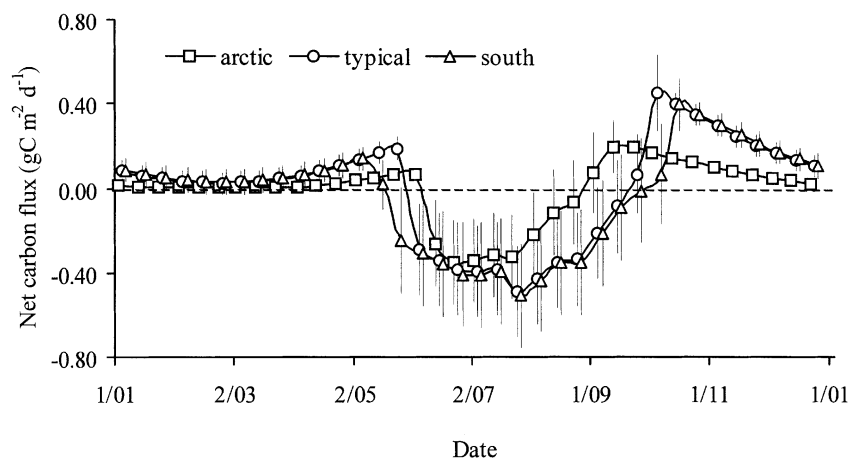


Fig. 9 Annual dynamics of net carbon fluxes in the main landscapes of Russian tundra using the present model

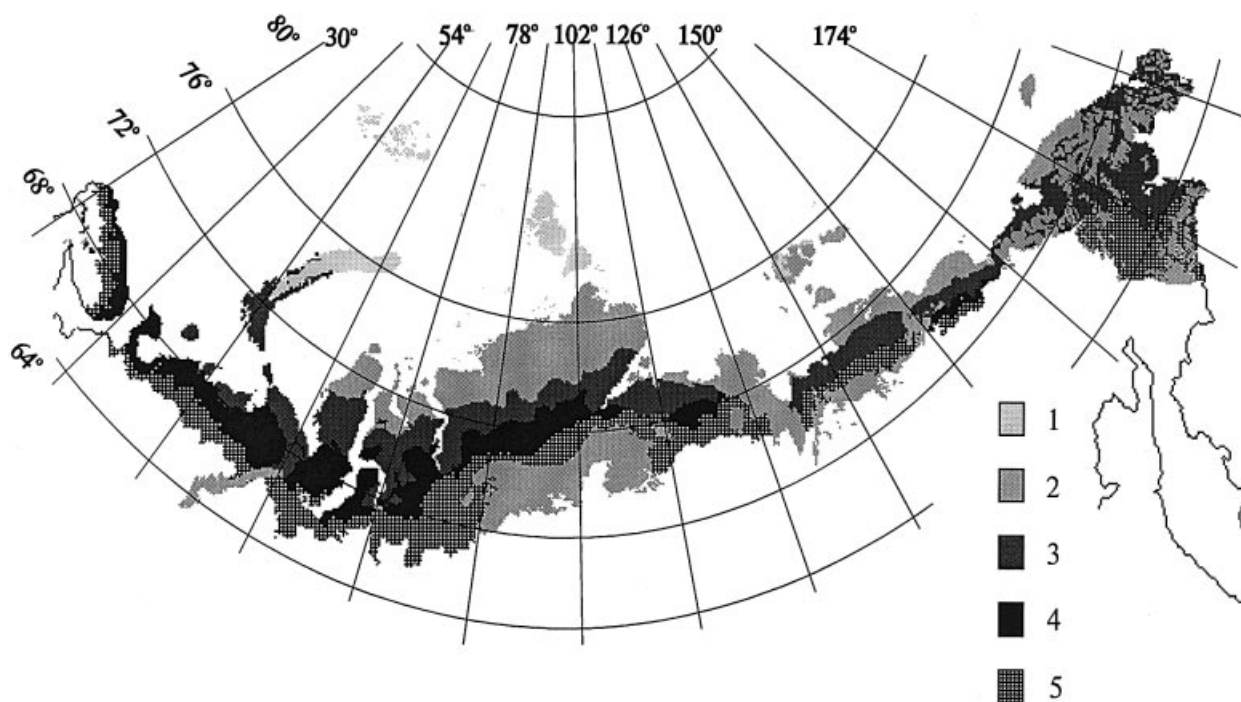


Fig. 10 The distribution of annual gross primary production (GPP) over the Russian tundra zone. 1, 0–15; 2, 15–150; 3, 150–300; 4, 300–450 $\text{gC m}^{-2} \text{ y}^{-1}$; 5, forest tundra landscapes. The map is in conic projection.

Table 1 Average and total values of gross primary production (GPP), gross respiration (GR) and net carbon flux (NF) in arctic (including polar deserts), typical, south and mountain tundras (including mountain polar deserts) and the entire Russian tundra zone

Tundra landscapes	Area (10 ⁶ ha)	GR (gC m ⁻² y ⁻¹)		NF (gC m ⁻² y ⁻¹)	GPP (10 ⁶ tC y ⁻¹)		NF (10 ⁶ tC y ⁻¹)
		Total	Cold season		Total	Cold season	
Arctic	68.8	71.8 ± 20.8	13.8 ± 5.4	-4.6 ± 24.5	-52.6 ± 15.0	9.5 ± 3.7	-3.2 ± 16.9
Mountain	45.3	86.1 ± 24.4	15.9 ± 5.3	-3.2 ± 29.0	-40.5 ± 12.2	7.2 ± 2.4	-1.5 ± 13.1
Typical	76.7	278.5 ± 34.4	33.2 ± 12.0	-1.5 ± 39.7	-214.7 ± 24.1	25.5 ± 9.2	-1.1 ± 30.4
South	44.4	388.0 ± 41.8	28.2 ± 12.5	-13.1 ± 48.8	-178.0 ± 18.4	12.5 ± 5.5	-5.8 ± 21.7
Russia	235.2	201.6 ± 14.9	23.3 ± 4.4	-4.9 ± 17.4	-485.8 ± 34.6	54.7 ± 10.4	-11.6 ± 40.8

Table 2 The area and annual values of gross primary production (GPP), gross respiration (GR) and net carbon flux (NF) of Russian tundra regions

Tundra landscapes	Area (10 ⁶ ha)	GR (gC m ⁻² y ⁻¹)		NF (gC m ⁻² y ⁻¹)	GPP (10 ⁶ tC y ⁻¹ per region)		NF (10 ⁶ tC y ⁻¹)
		Total	Cold season		Total	Cold season	
East-European	23.2	330.8 ± 41.8	28.8 ± 12.4	-3.5 ± 48.7	76.9 ± 9.7	6.7 ± 2.9	-0.8 ± 11.3
Polar Ural	3.7	155.7 ± 46.6	18.9 ± 10.4	9.8 ± 55.2	5.7 ± 1.7	0.7 ± 0.4	0.4 ± 2.0
Western islands of Russian Arctic	12.5	27.1 ± 24.0	3.1 ± 3.0	-11.0 ± 29.0	3.4 ± 3.0	0.4 ± 0.4	-1.4 ± 3.6
West Siberia	35.3	286.6 ± 44.2	28.0 ± 14.1	-4.8 ± 51.3	101.2 ± 15.6	9.9 ± 5.0	-1.7 ± 18.1
Central Siberia	76.1	187.0 ± 34.1	18.0 ± 9.6	-9.8 ± 39.9	142.2 ± 25.9	13.7 ± 7.3	-7.5 ± 30.4
Yakutiya	40.0	170.4 ± 39.4	26.9 ± 13.0	-0.6 ± 45.7	68.2 ± 15.8	10.7 ± 5.2	-0.2 ± 18.3
Eastern islands of Russian Arctic	4.5	41.1 ± 43.9	16.4 ± 12.3	-10.8 ± 51.4	1.8 ± 2.0	0.7 ± 0.6	-0.5 ± 2.3
Chikchi	39.9	187.4 ± 43.2	29.8 ± 13.0	0.3 ± 50.4	74.7 ± 17.2	11.9 ± 5.2	0.1 ± 20.1
Anadyr region							

responds to the estimates of annual fluxes for the whole Russian tundra zone.

The annual GPP of Russian tundra zone (for the area of 235×10^6 ha) was estimated at $-485.8 \pm 34.6 \times 10^6$ tC, GR as $+474.2 \pm 35.0 \times 10^6$ tC, and NF as $11.6 \pm 40.8 \times 10^6$ tC. The estimated carbon emission during the cold period constitutes 54.7×10^6 tC, or 11.5% of gross respiration. Therefore, according to the model, the annual GPP in the Russian tundra zone slightly exceeds RF by the absolute rate, which is not significant and hence corresponds to an equilibrium state of carbon balance.

The landscape computer map of the Russian tundra biome allows the spatial distribution of annual estimates of major carbon fluxes per unit area to be estimated. Because the obtained annual fluxes of GPP and respiration are very much interbalanced, in order to discuss the general patterns of carbon flux spatial distribution it is sufficient to analyse only the model-generated map of GPP. Figure 10 shows a more pronounced latitudinal distribution of GPP annual fluxes in Eastern tundra regions (East-European region, West and Central Siberia), that is not apparent in Western regions.

Comparing landscape types, the south tundra demonstrates the highest average rates of annual GPP and GR, whereas the arctic tundra has the lowest rates. Nevertheless, the landscape net carbon fluxes do not differ significantly (Table 1).

Comparing regions, the tundras of West and Central Siberia are the most valuable in overall carbon balance, providing 52% of total production and 51.3% of entire respiration (Table 2), which is result of the large areas occupied by these landscapes (47.3% of Russian tundra biome). Despite being relatively small in area (9.9%), the East European tundra (including Kola Peninsula) displays a rather intensive rate of carbon exchange, which results in its considerable partial participation in overall exchange processes in Russian tundra zone (16.0% for GPP and 16.2% for GR). This is mostly a consequence of its more southerly geographical position and the predominance of south shrub tundra in this region (Fig. 10). Chukotskiy Peninsula is situated even further south, but it demonstrates the lowest rate of carbon balance among all the main inland regions of Russian tundra zone (Table 2), which is readily explained by the influence of cold ocean streams, the peninsular position of the region, and predominance of mountain relief.

Perturbation experiments with the temperature

Processes of current global climate change could affect the present state of carbon balance in the Russian tundra biome. It was shown, that in some local regions of tundra biome, climate warming resulted in predominance of destructive processes over biomass production with

change from carbon sink to source (e.g. Oechel *et al.* 1993, 1995; Zimov *et al.* 1996; Zamolodchikov *et al.* 2000). The comparative analysis of air temperature trends shows that some of the Russian tundra regions might act as a carbon source to the atmosphere (Zamolodchikov *et al.* 1997).

We ran a simple computer experiment with our model, simulating the possible influence of temperature alterations on carbon balance. The input variable was mean air temperature within the warm period on a 10-d time-step. The length of the warm period, values of PAR and phytomass were kept as constants. The experiment revealed that while rates of production and respiration both follow the air temperature increase, the rate of respiration increase is somewhat faster, resulting in a carbon source to the atmosphere (Fig. 11). If the temperature elevation is 1°C compared to the long-term climate data used in the model, then the equilibrium state changes to a source. A further temperature elevation of 4°C above the initial long-term state in the model (the most likely increase following global warming; see: Mitchell *et al.* 1990) results in noticeable losses of carbon. In this case the model predicts an overall carbon emission in Russian tundras of about 60.7×10^6 tC, or $25.8 \text{ gC m}^{-2} \text{ y}^{-1}$. This value almost exceeds the estimate made for overall forest fire carbon emissions in Russia of $24\text{--}66 \times 10^6 \text{ tC y}^{-1}$ (Isaev *et al.* 1995).

Nevertheless we must emphasize that this simple experiment does not operate with such important controls of global warming as changes in evapotranspiration, hydrology, area ratio of different types of tundra landscapes, plant communities structure, and other factors. The use in the model of more recent climatic weather records may also be of help in understanding how Russian tundra ecosystems will react as a result of global temperature rise. This experiment shows only the

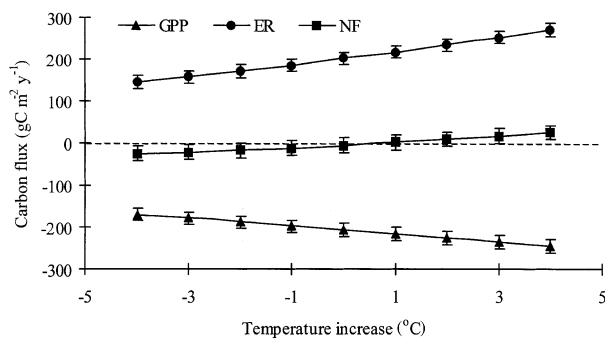


Fig. 11 Computer simulation of air temperature changes during the warm period of the year in Russian tundras. The dependent variables: GPP, gross primary production; GR, gross respiration; NF, carbon net flux

direct ecophysiological response of tundra to temperature changes. A long-term influence of elevated temperature may result in deep changes of soil carbon reserves and community structures with subsequent alteration of the phenomenological links between carbon balance and environmental controls. Therefore, these results have a only a short-term application.

Discussion

The present results and other known estimates for the Russian tundra zone

One way to verify the results of GIS modelling is to compare them with independent estimates of carbon parameters. For instance, the GPP of plant communities in the Kola Peninsula mountain tundras constitutes from -49 to -144 gC m^{-2} during the vegetative season (Politova & Lukiyanova 1991). The model gives an appropriate value of -101 gC m^{-2} for the mountain tundra landscape of the East-European tundra region. In the same plant communities the soil respiration varies from $+70$ to $+155 \text{ gC m}^{-2}$ (Shmakova 1994), which meets the model estimate of $+95 \text{ gC m}^{-2}$. The other example gives the values of gross respiration in typical tundra of Yakutiya, which is in the range of $290\text{--}320 \text{ gC m}^{-2}$ (Fedorov-Davydov & Gilichinskii 1993). The corresponding model value is $+279 \text{ gC m}^{-2}$.

The model GPP estimate of $485.8 \times 10^6 \text{ tC y}^{-1}$ corresponds closely to the earlier independent estimate of net primary production (NPP) in Russian tundras (Karelin *et al.* 1994: $293.0 \times 10^6 \text{ tC y}^{-1}$) calculated for the same landscapes and total area ($235 \times 10^6 \text{ ha}$). The NPP/GPP ratio of 0.603 is consistent with our experimental estimates 0.61 ± 0.07 ($n=6$) and with other data in the literature (0.5–0.6 by Kobak 1988; 0.62 by Politova & Lukiyanova 1991). This also shows good correspondence with the NPP value of $233.8 \times 10^6 \text{ tC y}^{-1}$ of Kolchugina & Vinson (1993) calculated for a smaller area ($214.2 \times 10^6 \text{ ha}$). The estimate of NPP for the area of $253.6 \times 10^6 \text{ ha}$ using a chlorophyll method was calculated at $190.2 \times 10^6 \text{ tC y}^{-1}$ (Mokronosov 1994), which is somewhat lower than our equivalent estimate. The above differences in zonal area estimates are a result of the different maps that the authors used (soil, vegetation, landscape or other maps).

Based on our unpublished experimental estimates, the respiration of all underground components of tundra ecosystems constitutes about 65% of gross respiration. In this case the overall rate of soil respiration in Russian tundras during the warm season might be as large as $272.7 \times 10^6 \text{ tC y}^{-1}$. This is considerably more than the estimate by Kudeyarov *et al.* (1995), calculated at $173 \times 10^6 \text{ tC y}^{-1}$ for the area of $350 \times 10^6 \text{ ha}$. The disagree-

ment is a consequence of the different length of the 'warm period' used in both studies (for our study it was longer). At the same time, we estimated the gross respiration of heterotrophs as $\text{ER} + \text{GPP} - \text{NPP} = 281.4 \times 10^6 \text{ tC}$, which meets the estimate by Kolchugina & Vinson (1993) of $229.1 \times 10^6 \text{ tC}$ for the area of $214.2 \times 10^6 \text{ ha}$.

This study resulted in determining the annual and spatial distributions of the overall biogenic macro-fluxes of carbon for the entire Russian tundra zone and different tundra landscapes as well. Both the regression-based equations and the GIS model of carbon fluxes were adequate means of reaching the goal of the study. Nevertheless, it is evident that a number of factors and processes affecting the interaction between climate change and the carbon cycle in tundras remained untouched in this study. The most important amongst these are concerns about the hydrology and the cryogenic processes in soils with permafrost, the direct influence of the increase of CO_2 concentration in the boundary atmospheric layer, and changes in cycles of biogenic chemical species. There are also several structural limitations of the model that are discussed below in order to identify priorities in future research.

The constraints of the model are largely a consequence of its empirical nature. Thus the regressions used are applicable only to the observed empirical ranges of the parameters. But we believe that the processes of global climate change might cause this majority to shift or create a new combination of carbon flux controls. Besides, the quality of source data is very important in empirical modelling. On the other hand, it is the empirical nature of the model that allows a better understanding of the limits of its application and domain. The actual set of driving factors, as in other models, reflects the state of our empirical knowledge of natural processes. New types of data or hypotheses will be necessary before we can substitute this dataset for another.

Linearity of the regression-based equations

At first glance it would seem that the simple multiple linear regressions used to simulate the carbon fluxes in the model are insufficient to describe such complex processes as GR and GPP. Respiration and photosynthesis are well known as nonlinear functions of temperature and light, respectively, which is another potential objection.

Our basic point is that there is no reason to use more sophisticated models if they do not provide any significant improvements in explanation of data variance over linear ones, as our analysis had shown. Possibly the general reason for sufficient explanatory capacity of linear equations is a relatively large time resolution (1 day). As regards the GPP equation (1), many ecosys-

tem models assume that canopy photosynthesis is usually light-limited and, hence, the rate of assimilation is a linear function of intercepted PAR flux (Jarvis & Leverenz 1983). Some studies in this field are convincing. The model by Leuning *et al.* (1995) proved that a summation of single leaf assimilation reactions in the canopy results in a linear function of available light on a daily time-step. A study by Waring *et al.* (1995) showed that a linear model of GPP vs. canopy PAR absorption is also applicable to canopies comprising many species, which was proved at monthly resolution.

Although it may be argued that these canopy effects were basically investigated in forests and agro-ecosystems, it is possible to apply these findings to tundra communities at our time resolution. Within the range of latitudinal distribution of tundra in Russia, the average PAR intensity during the growth season (7–10 MJ m⁻²d⁻¹) is substantially lower than the rates of photosynthetic light saturation in all studied tundra communities on a daily interval. Although accidental high PAR values and consequent nonlinear dependency of GPP light saturation are not uncommon on sunny days, small solar angle in tundra restricts potential period of light saturation, resulting in the reduction of nonlinear effects at a diurnal scale. This confirms the appropriateness of the GPP linear model in our study.

With respect to equation (2), the use of classic exponential dependencies of GR on temperature offer no significant advantages over linear models in the empirical range of diurnal air temperatures (0–20 °C). Furthermore, in most measurements of carbon fluxes this temperature span was smaller (1–12 °C). Within the real range of diurnal temperatures during the warm season this relationship is closely approximated by linear regression, and therefore it can be used in such a simplified form in the models with similar generalization. Nonlinear respiration effects are a result of sufficiently elevated diurnal temperatures.

Nevertheless, future model development in the use of nonlinear equations is needed to establish whether the present model is incapable of modelling dramatic climate changes.

Other controls of carbon fluxes

In the present model the length of growing season and aboveground phytomass dynamics correspond to long-term climatic conditions. However, both parameters can be easily tuned to specific cases by entering warm season length and seasonal dynamics of phytomass for a particular tundra ecosystem/landscape or region, a process which, in fact, we used to test a variety of regression models on the 1999 dataset.

In Russian (Fedorov-Davydov & Gilichinskii 1993; Christensen *et al.* 1998; Sommerkorn 1998) and other tundra regions (Flanagan & Veum 1974; Billings *et al.* 1982; Johnson *et al.* 1996; Oechel *et al.* 1998), a substantial dataset has been accumulated that reveals the strong influence of soil hydrological regime on ecosystem respiration. As the soil moisture or water table decreased, the respiration rate increased until limited by insufficient water content. The water table position determines the aeration of the upper soil horizons, and therefore has the highest potential here.

By contrast, our model explains gross ecosystem respiration satisfactorily using only air temperature and aboveground storage of living phytomass as controls. Soil hydrological regime (water table, soil moisture) and other potential respiration controls (e.g. thaw depth) were not included in the initial regression analysis because of the research goal. Besides, with the range of field datasets to hand, it was not feasible to obtain all the necessary data on seasonal dynamics of water tables and other factors for the complete list of ecosystems and regional landscapes in the Russian tundra zone.

We believe that the reasons for satisfactorily operation of limited number of respiration controls in the model are in the following. *In situ* studies of respiration fluxes at diurnal intervals have shown that it is necessary and sufficient to determine only water table and soil or air temperatures to explain most of the respiration variance (Flanagan & Veum 1974; Christensen *et al.* 1998; Oechel *et al.* 1998). Water table position is controlled significantly by air temperature at diurnal intervals (unpubl. data; Christensen *et al.* 1998) and yet the decline in its position results in a supplementary rise in near-surface soil temperature (Sommerkorn 1998). Air temperature rise directly increases the ecosystem respiration rate and also decreases the water table and soil moisture, resulting in aerobic respiration rise. Hence, both factors are acting in a very similar way. But more important, in our opinion, is the fact that biomass values of plant components in the regression equations are a specific characteristic of a particular ecosystem and its hydrology. For example, in wet biotopes with near-surface water tables, graminoid growth forms predominate, whereas in mesic ecosystems, deciduous or evergreen forms are the most common. The contributions of the latter components of aboveground living plant biomass to GR are the greatest. Hence, it follows that hydrology factor is implicitly included in the respiration equation terms.

Summary

The model presented is by no means universal. First of all it follows the requirements for handling a problem of spatial description of carbon fluxes at the macro-scale

(Russian tundra zone), while it can also run at a single site. Amongst the advantages of this model are the availability of used parameters and simplicity of its tuning and renewal for solving a specific problem. But when employing the model for prognosis or to other areas of tundra biome one should take into consideration the actual domain of the regression equations and temporal scale.

The model has potential for refinement by the equations alone or through the incorporation of new controls. The major constraint in this regard is the availability of data needed for spatial approximation. For instance, the position of the water table might be approximated by precipitation, solar radiation and thaw depth separately for mesic and wet habitats; start and length of growing season could be determined using the dynamics of snowpack and air temperature, etc. The intraseasonal dynamics of phytomass is the most serious obstacle to the application of the model to prediction. In the model's current state it is determined only by the length of growing season and the maximum seasonal storage of aboveground living biomass of plant growth forms in ecosystems. Therefore, an active search for the dependencies of plant growth forms and their biomass on intraseasonal environmental controls is of considerable priority in future model development.

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