ELSEVIER

Ecological Modelling 96 (1997) 191–210

ECOLOGICAL MODELLING

Testing the 'CENTURY' ecosystem level model on data sets from eight grassland sites in the former USSR representing a wide climatic/soil gradient

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Received 9 February 1995; accepted 5 August 1996

Abstract

Long-term ecological research under the International Biological Program and several other programs at research stations within the former USSR collected a large amount of data on phytomass, productivity and element cycling, together with climatic and soil regimes for various types of grassland ecosystems. This provides a unique opportunity to assess the performance of CENTURY across a wide environmental gradient from the luxuriant highly productive meadow-steppes of Central Russia to the ultracontinental steppes of Central Asia and the arid ephemeral grasslands in the Middle-Asian republics of the former USSR. The model simulations across this broad environmental gradient proved that the CENTURY ecosystem level model reproduced the seasonal, the mid-term, and in some cases the long-term dynamics of the live and dead aboveground phytomass of the grassland ecosystems in highly different natural-climatic zones of the former USSR. The r^2 for the comparison of observed and simulated live phytomass varies from 0.41 to 0.98 and the ratio of the absolute mean error of live phytomass to the peak seasonal live phytomass varies from 10 to 20%. The means and variation limits of the model are close to that of field data. The results suggest that many of the model discrepancies are a result of the fact that the model does not consider year-to-year changes in plant species composition. The measured Russian phytomass data for all of the sites are available on the World Wide Web. © 1997 Elsevier Science B.V.

Keywords: Grasslands; Ecological model; Nutrient cycling; Plant production

1. Introduction

A number of simulation models of grassland ecosystems have been developed during the past two decades, which encompass a variety of complexity, processes, data needs and data availability (Hunt, 1977; Innis, 1978; Gilmanov, 1978; Bashalkhanov, 1978; Innis et al., 1980; Pendleton et al., 1983; Parton and Singh, 1984; Shiyomi et al., 1985; Parton et al., 1987; Hunt et al., 1991). However, relatively few of these models have been rigorously tested across a range of environmental conditions. The need and desirability for model validation and sensitivity analysis has been repeatedly stressed in the literature on ecological modeling, however, most models have been tested over a limited set of conditions (Steinhorst et al., 1978; Innis et al., 1980; Rose, 1983;

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PII S0304-3800(96)00067-1

MacNeil et al., 1985). The ecosystem-level model CENTURY (Parton et al., 1987; Parton et al., 1988, Parton et al., 1995) has been successfully applied and tested across seasonal and long-term dynamics of plant production, decomposition and nutrient cycling in various grassland, agricultural and forest ecosystems in North and Central America, Africa, Europe, and Asia (Parton et al., 1993a; Parton et al., 1993b; Paustian et al., 1992; Sanford et al., 1991; Seastedt et al., 1994; Parton et al., 1995; Xiao et al., 1996). In this paper the results of CENTURY simulations of grassland ecosystems of European and Asian parts of the former USSR are presented.

As a result of long-term ecological research under the International Biological Program and other programs at research stations within the former USSR, a large amount of data on phytomass, productivity and element cycling, together with climatic and soil characteristics were collected, representing various types of grassland ecosystems. This data was used to assess grassland differences and the CENTURY model robustness to a wide environmental gradient from the moderate meadows of the North–West of European Russia and luxuriant highly productive meadow-steppes of Central Russia to the ultracontinental steppes of Central Asia and the arid ephemeroidal grasslands in the Middle-Asian republics of the former USSR.

The objective of this paper is to assess the capabilities of the CENTURY model to simulate the seasonal and long-term dynamics of the grassland ecosystems in different climatic and soil conditions across eight grassland ecosystems in the territory of the former USSR. These eight grassland ecosystems located at 7 research sites are representative of the natural gradient of climate and continentality from the moderate North–West of the European Russia to ultracontinental and desert steppes of Central Asia.

2. Methods

2.1. Model description

The CENTURY model is a general ecosystem level model (Fig. 1) that simulates plant production,

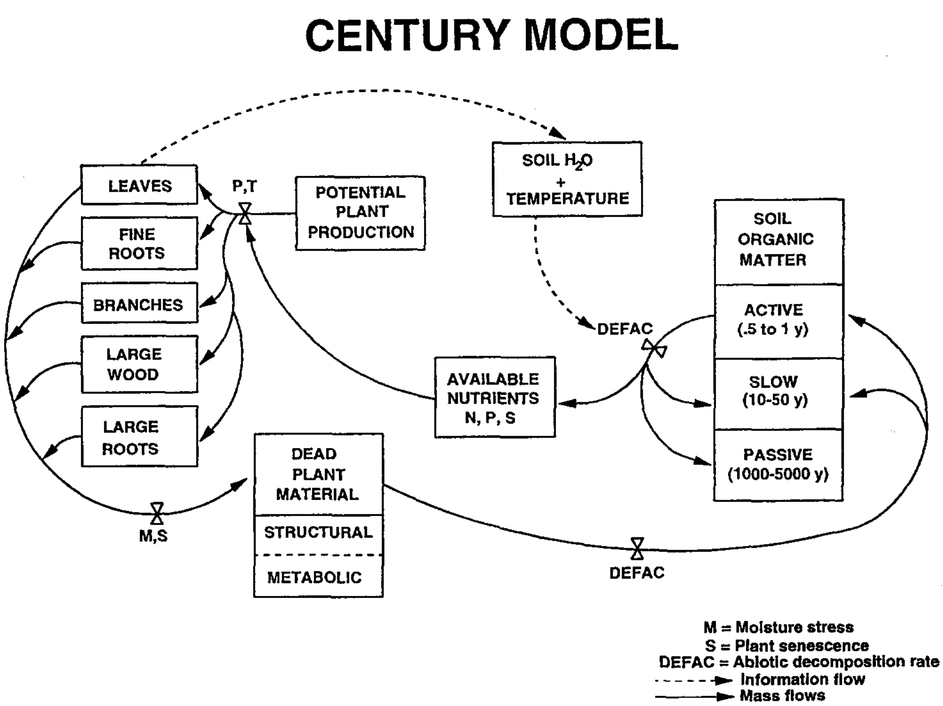

Fig. 1. Structure of the CENTURY ecosystem model.

soil water fluxes, soil organic matter dynamics and nutrient cycling for grassland, forest, savanna and agroecosystems (Parton et al., 1987; Parton et al., 1988; Parton et al., 1995). The model uses a monthly time step for most of the processes. Plant production is simulated by calculating the potential-plant production as a function of live leaf and monthly evapotranspiration and air temperature. Actual plant production is calculated by reducing the potential plant production in accordance with the available N supply and the specified carbon and nitrogen ratio of the different plant parts. The calibration of the plant production submodel is set to total plant production, allocation to above- and belowground components are based on environmental factors and species characteristics. The soil organic matter (SOM) model simulates organic matter dynamics by separating SOM into three pools (microbial biomass, slow and passive SOM) and simulating the cycling of SOM in these pools. The flow of SOM between pools is controlled by an abiotic decomposition factor which is calculated as a function of the actual evapotranspiration rate and monthly soil temperature. Nutrients are mineralized as a result of the cycling SOM in the different pools. Most of the carbon respiration and nutrient mineralization results from the turnover of the microbial biomass pool. The nutrient submodel also simulates nutrient loss due to nitrogen trace gas fluxes and leaching from the soil profile. The soil water model simulates monthly soil evaporation, rain interception by plants, and transpiration (Parton et al., 1993a; Parton et al., 1993b). These processes include the impact of live and dead plant biomass on the water fluxes. The model also simulates watershed stream flow and uses monthly average maximum and minimum daily air temperature and monthly precipitation as the driving variables for the model.

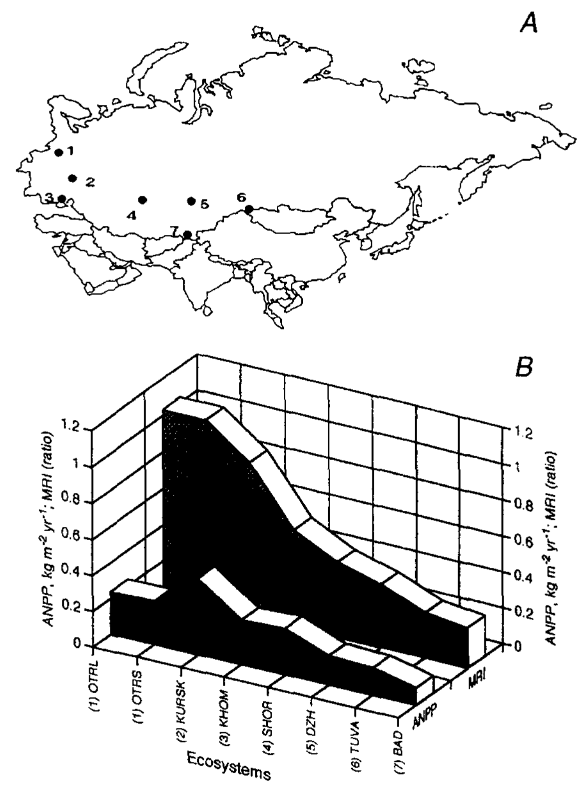

Fig. 2. Geographical distribution of the grassland ecosystems used for testing of the CENTURY model: (1) OTRL – loamy upland meadow and OTRS – sandy upland meadow; (2) KURSK – virgin meadow steppe near Kursk; (3) KHOM – typical steppe 'Khomutov'; (4) SHOR – dry continental steppe 'Shortandy'; (5) DZH – desert steppe 'Dzhanybek'; (6) TUVA – ultracontinental steppe 'Tuva'; (7) BAD – desert 'ephemeretum' grassland 'Badkhyz' (A). Arrangement of the validation sites with different aboveground net primary production ANPP (kg m^{-2} yr^{-1}) along the axis of the moisture/radiation index (MRI) = $(P * L)/(100 * R_b)$ (B).

3. Description of sites

The geographical distribution of the 7 grassland validation sites encompass the major grassland types of Eurasia (Fig. 2A), and their principle ecological characteristics are summarized in Table 1. The sites selected encompass an extremely wide climatic gradient in the direction of increasing maximum summer temperatures and continentality and decreasing precipitation from the North–West to South–East to the center of Eurasia. As shown by Grigoryev (Grigoryev, 1954; Grigoryev and Budyko, 1956), a useful bioclimatic index of ecosystem productivity is the ratio of yearly radiation balance of the site R_b (MJ m^{-2} y^{-1}) to the amount of energy, needed for evaporation of the yearly precipitation $(0.01 * P * L)$, where P is measured in cm y^{-1} and $L = 2464$ MJ m^{-2} cm^{-1}. Using for convenience the reciprocal value, which we will call the 'moisture/radiation index' (MRI) $= (P * L)/(100 * R_b)$, it is clear that these sites cover a broad range of ecosystem productivity relative to climate and soils (Fig. 2B). From the desert grassland of Badkhyz on the serozem soil to the meadow steppe near Kursk with rich chernozem soil the aboveground primary production ANPP is practically directly proportional to the MRI. The decrease of productivity from meadow steppe to the moderate meadow near Otradnoe is caused by the substantial decrease of soil fertility and deterioration of the hydrothermal conditions of the soddy-podzolic soil compared to the rich chernozem (Fig. 2B).

The Otradnoe site, location 1 (Fig. 2) represents the ecosystem of an upland meadow in the moderate climate. The site was established during the IBP period at the 'Otradnoe' research station of the V.L.

Table 1
Principal ecological characteristics of the selected grassland ecosystems of the climatic/soil gradient in the former USSR

Characteristics	Loamy meadow (OTRL)	Sandy meadow (OTRS)	Meadow steppe (KURSK)	Typical steppe (KHOM)	Dry steppe (SHOR)	Continental steppe (DZH)	Ultracontinental steppe (TUVA)	Desert steppe (BAD)
Longitude (° East)	30.25	30.25	36.5	38	71	46.78	94.42	62
Latitude (° North)	60.83	60.83	51.67	47.17	51.67	49.33	51.83	35.68
Altitude (m)	50	50	250	75	367	20	800	700
Growing season (days)	165	165	190	195	168	198	115	291
Radiation balance (MJ/m^2/yr)	1296	1296	1610	2007	2049	1923	2091	2906
Moisture/radiation index	1.03	1.03	0.86	0.54	0.42	0.35	0.25	0.23
Mean annual temperature (°C)	3.6	3.6	5.6	9.4	0.7	6.9	−4.5	14.6
Minimum annual temperature (°C)	−12.6	−12.6	−12.6	−13	−22.9	−20.7	−39.2	−15
Maximum annual temperature (°C)	22.2	22.2	24.7	31.4	25.7	29.7	26.7	40.2
Temperature amplitude (°C)	34.8	34.8	37.3	44.4	48.6	50.4	65.9	55.2
Precipitation (cm/yr)	54.3	54.3	56	44.1	35.1	27.4	21.4	26.6
Sand (%)	42	80	32	20	36	28	74	68
Silt (%)	40	12	31	28	27	28	17	23
Clay (%)	18	8	37	52	37	44	9	15
Humus (kg C/m^2/20 cm)	5.78	3.78	10.43	6.93	5.6	3.15	4.03	1.16
Humus (kg C/m^2/100 cm)	7.44	5.74	34.5	23.5	18.8	7.85	8.43	—
Soil nitrogen (kg N/m^2/20 cm)	0.46	0.28	0.91	0.58	0.5	0.34	0.43	0.14
Soil nitrogen (kg N/m^2/100 cm)	0.63	0.39	2.9	2.32	1.4	0.95	0.99	—
Soil acidity (pH)	5.2	5	6.3	7.8	7.6	7.8	7.3	8
Cation exchange capacity (meq./100 g)	18	13	53	30	35	20	17	12
Aboveground live phytomass (g DW/m^2)	244	277	362	340	142	137	103	69
Standing dead (g DW/m^2)	64	62	344	90	152	32	57	42
Litter (g DW/m^2)	103	121	424	240	376	—	38	132
Belowground phytomass (g DW/m^2)	508	627	910	1675	1686	1750	725	1180
Belowground mortmass (g DW/m^2)	255	323	1370	792	1747	—	3915	—
Aboveground production (g DW/m^2/yr)	269	342	774	460	335	201	150	100
Belowground production g DW/m^2/yr)	507	794	1700	—	1745	—	—	1745
Net primary production (g DW/m^2/yr)	776	1136	2474	—	2080	—	—	2080
Root/shoot ratio	2.08	2.26	2.51	4.93	11.87	12.77	7.04	17.1
BNPP/ANPP ratio	1.88	2.32	2.2	—	5.16	—	—	8
Belowground dead/live phytomass ratio	0.5	0.52	1.51	0.47	1.04	—	5.4	5.4
Soil C/N ratio	11.81	14.72	11.9	10.13	13.43	8.26	8.52	8.67

Komarov Botanical Institute of the Russian Academy of Sciences and is located at the Karelian peninsula 100 km to the north of St. Petersburg (Guricheva et al., 1975; Ponyatovskaya, 1978). The 'Otradnoe' site provided grassland data from two different soil textures: a loamy soil ('OTRL') and a sandy soil ('OTRS'). The loamy meadow 'OTRL' is an upland plant community on heavy-loamy soddy-podzolic soil (Table 1). The plant community comprises 61 vascular species, the grasses *Agrostis tenius*, *Anthoxanthum odoratum*, *Festurca rubra*, the forbs *Alchemilla monticola*, *Centaurea jacea*, *Achillea millefolium*, *Lathyrus pratensis*, and the legume *Trifolium pratense*.

The sandy meadow site, OTRS, is located on a sandy soddy-podzolic soil (Table 1). The species richness is 47 vascular species, the grasses *Alopecurus pratensis*, *Agrostis tenius*, *Anthoxanthum odoratum*, the forbs *Alchemilla monticola*, *Achillea millefolium*, *Centaurea jaccea*, and the legumes *Trifolium repens* and *Vicia cracca* dominating among them.

The Kursk site is a virgin meadow steppe (Table 1) of the Central-Chernozem Natural Reserve, Kursk Region, Russia (site 2, Fig. 2). The rich loamy chernozem soil is one of the most productive upland grassland ecosystems of Russia (Gilmanov and Bazilevich, 1983; Bazilevich and Gilmanov, 1984) and has been studied for many years (Semyonova-Tyan-Shanskaya, 1966; Afanasyeva, 1966; Utekhin, 1977; Khoang-Tyung, 1975; Gilmanov and Bazilevich, 1983; Bazilevich et al., 1988). Dominant species of this plant community include *Bromus riparius*, *Stipa pennata*, *Poa angustifolia*, *Agropyron intermedium*, *Filipendula hexapetala*, *Fragaria viridis*, and it is noted by its high species richness, with up to 77 species per 1 m^2 and 120 species per 100 m^2 (Alekhin, 1934).

The typical steppe ecosystem with calcareous chernozem soils is represented at the permanent research station 'Khomutovskaya steppe' (Table 1, the Ukrainian Steppe Natural Reserve, Donezk Region, Ukraine; site 3, Fig. 2). This ecosystem was once widely distributed over the Black Sea Lowland. The species richness of this plant community is 23 species per 1 m^2 and 60 species per 100 m^2, and is dominated by *Stipa lessingiana*, *Stipa capillata*, *Festuca sulcata*, *Poa angustifolia*, *Linozyrus villosa*, *Medicago romanica*, *Salvia nutans*. The natural conditions, phytomass and productivity dynamics of this ecosystem are described by Bystrickaya and Osychnyuk (1975).

The ecosystem of the 'Shortandy' site (Table 1), which is characteristic of a dry continental steppe, is representative of the semiarid continental grass-forb steppes of the Northern Kazakhstan (site 4, Fig. 2), found on the southern chernozem soils (cf. Titlyanova et al., 1984; Shatokhina, 1988). The dominant plant species are *Stipa zalesskyi*, *Helicotrichon desertorum*, *Stipa lessingiana*, *Peucedanum alsaticum*, *Jurinea multiflora*, *Salvia stepposa*, *Artemisia dracunculus*, *Galium verum*, and the species richness is 12–20 species per 1 m^2 and 42–62 species per 100 m^2.

The 'Dzhanybek' research station (site 5, Fig. 2), located on the Near Caspian Lowland, is representative of semidesert steppes on the heavy light-chestnut soils (Table 1). The most abundant species of the zonal ecosystem of this landscape are *Tanacetum achilleifolium*, *Agropyron desertorum*, *Poa bulbosa*, *Festuca valesiaca*, *Kochia Prostrata*, and the total species richness of the community is as high as 40 species of vascular plants (Gordeeva and Larin, 1965; Olovyannikova, 1976; Rohde, 1974; Abaturov, 1984; Gilmanov and Ivaschenko, 1990).

The 'Tuva' research station (site 6, Fig. 2) belongs to the region of ultracontinental semiarid and cryoarid steppes of the inland depressions of Central Asia, formed on the light-textured chestnut soils (Table 1). The plant community is dominated by *Agropyron crystatum*, *Cleistogenes squarrosa*, *Festuca valesiaca*, *Helictotrichon altaicum*, *Koeleria cristata*, *Stipa krylovii*, *Carex supina*, *Potentilla bifurca*, *Artemisia commutata*, *Artemisia frigida*, *Caragana splendens*. The data on natural conditions, soils, composition and productivity of plant and animal communities were presented by Nosin (1963), Volkovincer (1978), Gorshkova (1982), Gorshkova (1986), Stebayev et al. (1964), Stebayev (1976), Stebayev (1986), Stebayev and Pshenicyna (1984).

The last of the sites selected is the 'Badkhyz' Natural Reserve (Site 7, Fig. 2) representing the ephemero-ephemeroidal desert grasslands on the serozem soils of the foothills of the mountains of the Middle-Asian Republics of the former USSR (Table 1). This desert grassland type is also known as the 'ephemeretum ecosystems'. The soils belong to the serozem type with light loam or sandy texture, high carbonate content, poor in humus and mineral elements for plant nutrition. The species richness of the plant community amounts to 64 vascular species, with predominance of *Poa bulbosa*, *Carex pachystylis*, *Onobrychis pulchella* and several desert annuals. The long-term observations on climate, soils and productivity of the ephemeretum ecosystem (Nechaeva et al., 1971; Artykov, 1975; Kamelin and Rodin, 1989) of the Bakhyyz Natural Reserve in Southern Turkmenistan were used to test the model.

All the selected ecosystems are located at the upland geomorphologic positions and are considered as the zonal climatic climaxes of the corresponding regions, excluding the meadow ecosystems of the 'Otradnoe' site in the southern taiga subzone of the forest zone. The methodological aspects of field experimental studies of biomass and production of grassland ecosystems of the Former Soviet Union were summarized in a special paper by Titlyanova (1988). The methods of field measurements of above- and belowground biomass in Russian grasslands are based on the harvest technique and with respect to sampling area, replication, etc., are very close to the methods used by western ecologists during IBP studies (e.g., Sims and Coupland, 1979; Coombs et al., 1985). The Russian approach to estimation of the annual production of grassland plant communities (with subdivision on aboveground and belowground components) is based on a special calculation procedure utilizing data of repeated (usually with 2 week time step) sampling during the season of live, standing dead and litter fractions of phytomass. According to Titlyanova (1988, p. 8) this method of calculation gives the estimates of production which are 1.6 to 2.0 times higher than the seasonal maximum of the standing crop of the corresponding phytomass fraction. The validation data are available on a World Wide Web site: for the summary data: http://www-eosdis.ornl.gov/npp/npp-summ.html and for the site level validation NPP data: http://www-eosdis.ornl.gov/npp/npp-summ.html.

4. Site level model parameters

To test the potential of the CENTURY model to simulate the seasonal and year-to-year dynamics of production and decomposition processes, the model was parameterized for each site and then was run with the meteorological data for those years, for which the phytomass and/or productivity dynamics data were available. The main goal of the parameterization procedure was to achieve reasonable performance of the model on different data sets keeping as many parameters as possible at their default values (cf. the CENTURY manual; Parton et al., 1992). There was no attempt to separate data for parameterization of the model and independent validation of the model because the length of the data sets ranged from 3 years to > 30 years. It is also important to note that we analyzed the data sets extensively prior to the model parameterizing process and thus made it difficult to claim that portions of the data are independent data sets.

The parameters of the CENTURY model are subdivided into two sets. The first set, contained in the CENTURYM.FIX file (Parton et al., 1992) include the firmly determined parameters, which values are rarely changed. However, for this analysis we had to modify 3 parameters in the CENTURYM.FIX file. These were the temperature response functions for plant production and decomposition: ppdf(1) – optimum temperature for production; ppdf(2) – maximum temperature for production; and topt – optimum temperature for decomposition of the organic matter (Table 2). The climatic gradient of mean annual temperature ranged from −4.5°C (Tuva) to 14.6°C (Badkhyz). The plant and soil biota have developed under these different climatic conditions.

Table 2
Parameters of temperature control of production process in the model in relation to the biotemperatures of the sites and values for optimum soil temperature for decomposition (topt): (A) optimum temperature for production, ppdf(2); biotemperature is the average temperature of the actual growing season

Site	Biotemperature	ppdf(1)	ppdf(2)	topt
TUVA	13.1	15	32	33.5
BAD	13.53	15	32	32.0
OTRL	13.62	14.8	34.7	32.0
OTRS	13.62	15	35	30.0
SHOR	14.83	15	32	33.5
DZH	14.92	22	45	35.0
DURSK	15.11	16	35	33.5
KHOM	16.17	22	45	33.5

Table 3
Parameters used for tuning the CENTURY model to adequately simulate the behavior of grassland ecosystems from different research sites

Parameters	Sites								
	OTRL	OTRS	KURSK	KHOM	SHORT	DZH	TUVA	BAD	default
epnsf(1)	−0.86	−0.86	−0.86	−0.86	−0.86	−0.86	−0.86	−0.86	−1.32
epnsf(2)	0.05	0.10	0.12	0.25	0.12	0.11	0.05	0.05	0.033
fallrg	0.30	0.40	0.20	0.40	0.10	0.30	0.15	0.15	0.20
fsdeth(1)	0.20	0.10	0.20	0.15	0.20	0.07	0.20	0.20	0.20
grdr	0.15	0.15	0.10	0.10	0.045	0.10	0.05	0.05	0.12

These temperature parameters control the rates of production and decomposition and adjustments were made to accommodate the unique features of these ecosystems. For this purpose, we calculated the average biotemperature of each site, i.e., the average temperature of the actual growing season rather than using the mean annual temperature. As can be seen from Table 2, the optimum temperatures for production ppdf(1) derived by CENTURY are in general agreement with the biotemperatures of the sites. The sites with the higher biotemperatures, e.g., Khomatov and Dzhanybek, used the higher values of ppdf(1) and ppdf(2). The latter has a mean annual temperature 14.6°C, but during the growing season from February to April (early May) the average temperature is only 13.5°C.

The default 'optimum' temperature for decomposition in CENTURY is topt = 35°C. Table 2 shows that the estimated topt values are generally lower. This is consistent with recent information (Paustian et al., 1992) showing that the CENTURY model tends to underestimate decomposition rates and overestimate soil carbon levels for high latitude continental sites (similar to most of the sites in Russia) with low air temperatures. Analysis of the model shows that the CENTURY soil temperature decomposition curve underestimated decomposition rates for temperatures less than 10°C. Paustian et al. (1992) suggest that this error can be eliminated by reducing the value of topt and thus increasing the decomposition rates for low soil temperatures.

The second group of parameters of the CENTURY model, introduced to the model via the SITENAME.DAT parameter file, contains the site specific parameters. Table 3 presents the input site parameters of the CENTURY model, which were used to simulate production/decomposition processes in the former USSR grassland sites. The parameters fsdeth(1), fallrg and grdr, designate the monthly rates of shoot death, transfer of standing dead into litter and root death. These parameters are based on site characteristics reflecting plant dynamics corresponding to environmental conditions at each site. For example, the lowest root death rates for Shortandy, Tuva and Badkhyz sites are in compliance with the empirically observed absolute and relative (to aboveground phytomass) amounts of belowground biomass in these ecosystems, while the greater values of grdr for moderate meadows in Otradnoe correspond to lower reserves and higher turnover rate of root biomass in moderate grasslands compared to semi-arid and especially continental grasslands (Miroshnichenko, 1975; Titlyanova, 1977; Shatokhina, 1988).

One of the key controls in the CENTURY model is the amount of N inputs an ecosystem receives. CENTURY uses a linear relationship with epnfs(1) being the y-intercept and epnfs(2) the slope term

Table 4
Model estimates of the annual N-fixation rate of various grassland ecosystems of the former USSR in relation to empirical data on the reserves of total soil nitrogen

Site	Nsoil100 ($g\ N/m^2$)	PotNfixMod ($g\ N/m^2/yr$)
OTRL	0.630	2.1678
OTRS	0.390	4.7072
KURSK	2.900	8.6082
KHOM	2.320	11.6556
SHOR	1.400	4.112
DDZH	0.950	2.5144
TUVA	0.990	0.6572
BAD	0.250	0.512

used with the amount of rainfall to determine N inputs via biological soil N-fixation. These grassland ecosystems are characterized by the presence of N-fixing plants and this is reflected in the range of soil organic N levels (Table 4). In order to account for this apparent higher level of N inputs, the values of epnfs(1) and epnfs(2) were elevated (Table 3). The epnfs(1) is increased by 0.36 and the slope term is elevated and reflects the higher soil N-fixation found in Eurasia steppe systems (Umarov, 1986).

5. Model assessment

Though several dozens of state variables are calculated by CENTURY, we shall focus our attention on the dynamics of various carbon pools, especially the aboveground live phytomass. In order to obtain a more detailed assessment of the model's capability to simulate the seasonal course of phytomass dynamics in the years with different meteorological regimes we use two indices, which are often applied to evaluate agreement between model results and measured data:

(I) the mean absolute deviation D_{abs}

$$D_{abs} = \frac{1}{n} \sum_{i=1}^{n} |X_{mod}(t_i) - X_{dat}(t_i)| \tag{1}$$

where variables X_{mod} and X_{dat} designate the model and measured values of the same property, and t_i ($i = 1, \ldots, n$) are the moments of time, for which observation data are available;

(ii) the slope coefficient, b, in the formal regression equation of the field data on the corresponding model values:

$$X_{dat} = a + bX_{mod} \tag{2}$$

Under the assumption of full model adequacy the intercept $a = 0$ and the slope $b = 1$. Therefore, the test criteria will be made relative to the closeness of b to 1. Since the first index (D_{abs}) is biased for point-to-point comparison, and the second index (b) is more characterizing the general pattern of points on the (X_{mod}, X_{dat}) plane, combined use of both indices will help to assess the agreement between model and data more comprehensively.

6. Results

6.1. Otradnoe – OTRL and OTRS

For the loamy meadow 'OTRL' the field data are available for the 5 year period 1967–1972. The model simulation behavior corresponds well to observed data (Fig. 3A): the model curve not only stays within the limits of the seasonal variations of phytomass reserves, but it also accurately describes periods of beginning of the spring growth and autumn senescence. The mean absolute deviation of empirical data from model is $D_{abs} = 36$ g/m^2. It is only in the last year (1972) that the model does not reach the highest observed value of $G_{max} = 335$ g/m^2. One might explain this by the unusually high temperatures during the summer of 1972: while for 1967–1971 the mean June, July and August temperatures were 15.7, 16.8 and 16.1°C, for the 1972 the corre-

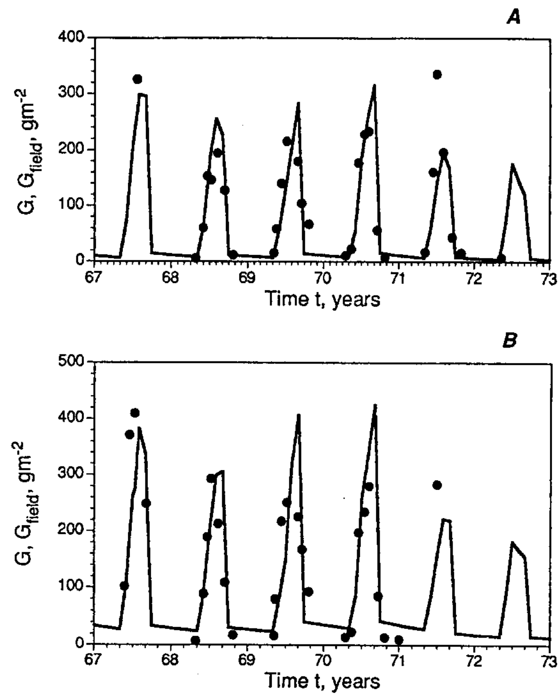

Fig. 3. Dynamics of the aboveground live phytomass G (g m^{-2}) of (A) the loamy meadow OTRL ($D_{abs} = 36.0$ g m^{-2}) and (B) the sandy meadow OTRS ($D_{abs} = 54.1$ g m^{-2}) for the 1967–1972 period. Points – field data after Guricheva et al. (1975) and Ponyatovskaya (1978); curves – simulation results with real meteorological data for the same period.

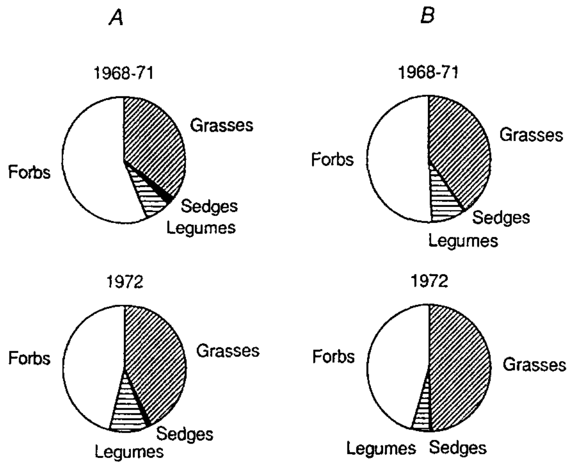

Fig. 4. Changes of the composition of the plant community of the loamy meadow OTRL (A) and sandy meadow OTRS (B) in the hottest year 1972 compared to average data for more typical 1968–1971 period (after data by Ponyatovskaya, 1978).

sponding figures amounted 17.7, 21.7 and 18.6°C, i.e., were 2 to 5°C higher. This obviously resulted in considerable changes in the composition of the plant community, as it can be seen from the Fig. 4A, illustrating the increasing role of grasses and legumes and decrease of sedges and forbs. Since the present version of CENTURY is unable to take into consideration such shifts in the community composition, the parameters, which ensured successful model behavior for majority of typical years, did not allow agreement for a year with exceptional weather. For the whole 5 year long period of observations the error of the model is equal to 10.7% of the maximum phytomass value of $G_{max} = 335$ g/m^2, which is comparable to the precision of field phytomass estimates. The second index of model performance — the slope b of the regression line of field versus model data — is 0.98.

For the sandy meadow 'OTRS', where the field data for phytomass and production dynamics are available, the agreement between the empirical and model data is no less acceptable than for the loamy meadow (Fig. 3B): the mean deviation $D_{abs} = 54$ g/m^2 or 13.2% of the maximum amount $G_{max} = 409$ g/m^2; the regression slope of G_{field} versus G_{model}, $b = 0.95$, is also very close to 1.0. It is known, that with respect to the thermal regime the sandy soils are 'warmer' than loamy or clay soils. Therefore, discrepancies between field data and the model in the 'hot' 1972 year in this ecosystem are not so pronounced, as in Fig. 3A for the loamy meadow. The pie-charts of Fig. 4B show that the changes of the community composition of the sandy meadow in 1972 compared to period 1968–1971 are less expressed, and shows only a slight increase in grasses.

6.2. Kursk – KURSK

The 30 year (1954–1983) time series of above-ground phytomass (Fig. 5) of the Kursk site covers a wide diversity of weather conditions. The peak phytomass range from 202 g/m^2 in 1963 (a cold winter and spring followed by a dry and hot May), to a high of $G_{max} = 770$ g/m^2 in 1982 (favorable weather in all seasons of the year). Consequently, this Kursk data set provides a good opportunity for testing the CENTURY model, and the results of the testing appeared to be quite good. For the whole 30 year Kursk phytomass data set the mean absolute deviation, equal to $D_{abs} = 133$ g/m^2 seems, at the first glance, rather high compared to other sites. But taking into account the maximum phytomass $G_{max} =$ 770 g/m^2 we find that the error is only 17.3% of the maximum value, which is acceptable for the model with monthly time step designed to describe the long-term dynamics.

With this accuracy level for the whole 30 year simulation interval (1953–1983, Fig. 5) there are sufficiently long series of years, e.g., 1967–1973 (seven years) or 1976–1981 (six years), when the agreement between the model and data is substantially better. For instance, for 1967–1973 the error is only $D_{abs} = 92$ g/m^2 for the period 1976–1981 it also is appreciably lower, than for the whole data set and equals $D_{abs} = 98$ g/m^2. On the other hand, at 11 of 30 years the differences between data and model exceed 30% of G_{max}, while for 6 years, namely, 1954, 1963, 1966, 1974, 1981, and 1982, the discrepancy is $\geq 50\%$ of G_{max}.

Among the multitude of possible reasons for such disagreements between the data and the model (including the sampling error with its instrumental and spatial variability components, the latter being rather high in the virgin meadow steppe), one should pay attention to two particular moments, related to the modeling procedure itself. The first is the problem of

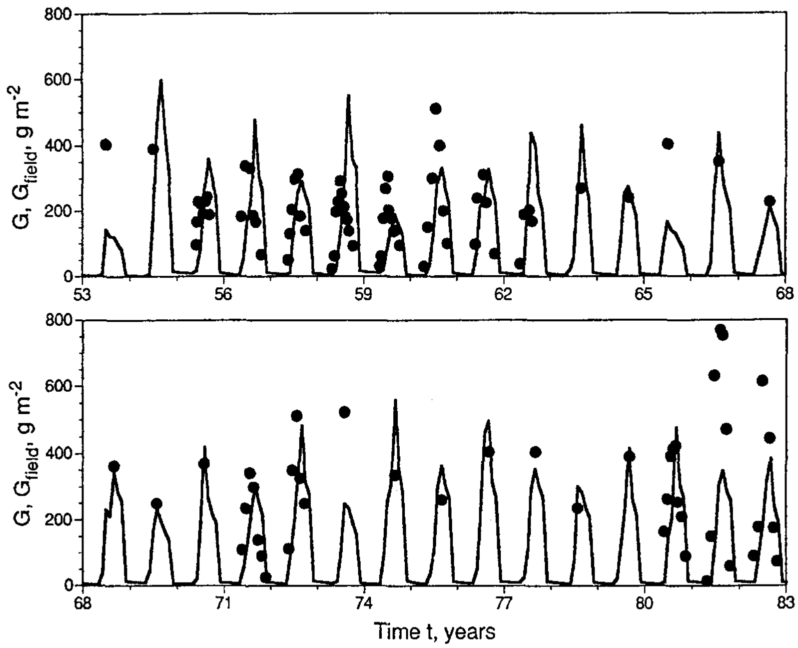

Fig. 5. Dynamics of the aboveground live phytomass G (g m^{-2}) of the meadow steppe ecosystem near Kursk (KURSK) for the 1954–1983 period. Points – field data after Semyonova-Tyan-Shanskaya (1966), Utekhin (1977), Khoang-Tyung (1975), and Bazilevich et al. (1988); curve – simulation results using the real meteorological data for the same period. $D_{abs} = 133.0$ g m^{-2}.

the species and functional diversity of the plant community, which was already mentioned for the moderate meadow ecosystems. It is obvious that for such a rich community as the virgin meadow steppe the highly aggregated CENTURY model has difficulty in representing the whole variety of responses of the meadow steppe community to the different weather regimes during the entire 30 year simulation period. It is very probable that during such a long period a substantial change of the relative abundance of species and groups of species. Differences in their hydrothermal and production parameters may have resulted in differential responses of the community to the meteorological conditions of different years.

The second circumstance is connected with modeling of the processes of plant phenological development, which in CENTURY is prescribed by three numerical parameters, determining the beginning and the end of the period of vegetative growth, and the beginning of the senescence of the shoots. Thus, as was already pointed out earlier, the year 1963 was marked by the lowest value of the seasonal phytomass maximum, $G_{max} = 202$ g/m^2. Very probably, this was caused by the negative influence of cold spring and subsequent dry and hot early summer on the development of the majority of the species of the plant community. The abundant rains in late June and July were not able to help to restore production. But the CENTURY model, based on the assumption of the initial role of the hydrothermal factors and nitrogen supply in determining plant production, quite logically is predicting for this year much a higher harvest of $G_{max} = 427$ g/m^2. The regression coefficient on the scatter diagram of G_{field} versus G_{model} for the Kursk site, which includes 108 points, has a lower value of $b = 0.91$; the $R^2 = 0.67$ also indicates noticeable scattering.

6.3. Khomutov – KHOM

Detailed observations of phytomass dynamics at the typical steppe ecosystem of the Khomutov site were conducted during the four-year period 1967–1970 (Fig. 6). The visual agreement between model and field data for this case is confirmed by the numerical indexes: $D_{abs} = 97.8$ g/m^2 (or 20.8% of

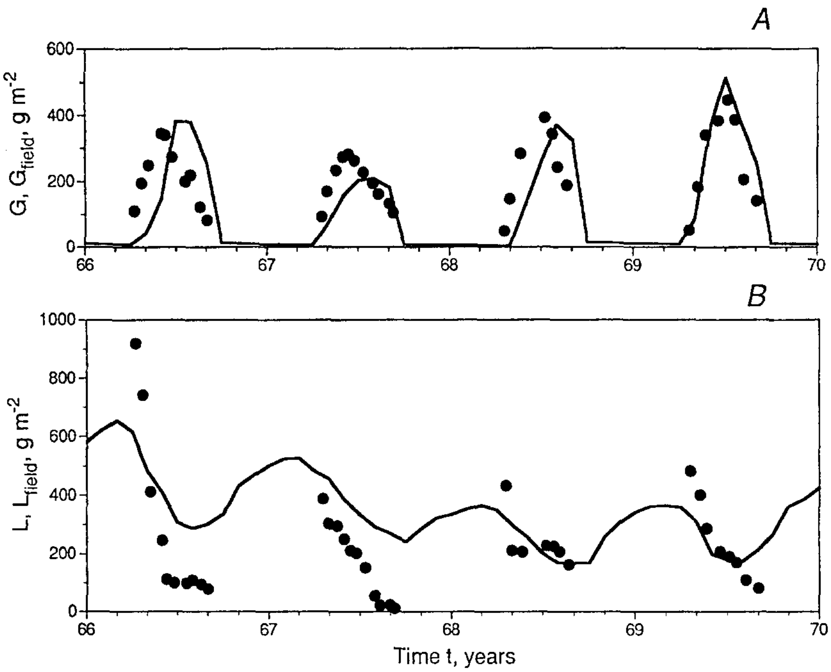

Fig. 6. Dynamics of the aboveground live phytomass G (g m^{-2}) (A), $D_{abs} = 98.0$ g m^{-2}, and the aboveground litter mass L (g m^{-2}) in the typical steppe ecosystem of the Khomutov site (KHOM) for the 1966–1970 period. Points – field data after Bystrickaya and Osychnyuk (1975); curve – simulation results using the real meteorological data for the same period.

G_{max}), $b = 0.88$, and $R^2 = 0.8$ ($n = 37$). One can notice both the successful representation of the numerical values and ranges of variation, and the pattern of changing the phytomass maxima during the period of simulation. The mean absolute deviation between the corresponding maxima of the model and the field data, D_{max}, which also may be used as a useful index of model performance for the Khomutov site, is less than D_{abs} and is equal to 46.9 g/m^2. Unfortunately, the phytomass data for the year 1965, for which the model is giving the unusually high value $G_{max} = 636$ g/m^2, are not available. But to verify this prediction we can use the available data on the spring amount of litter in 1966, when in April the amount was found to be 919 g/m^2. This high level of litter is significant, since most of the litter is decomposed within two years. This taken with the observation that the average amount of litter for the years of observation was approximately 300 g/m^2 (cf. Fig. 6B) leads to the conclusion that 1965 was a highly productive year and led to a substantial input to the litter compartment. So inference provides justification that the highest peak of phytomass, predicted by the model, could really have taken place in 1965.

Thus, remembering the limited potential of CENTURY to describe spring phenology, which is especially pronounced for 1968 (Fig. 6A), we still can qualify the model as sufficiently adequate for the purpose of simulating the year-to-year dynamics of phytomass in the typical steppe ecosystem under variable meteorological conditions.

6.4. Shortandy – SHOR

For the dry continental steppe of the Shortandy research station in northern Kazakhstan the data on phytomass and production were collected during 1975–1979 (Shatokhina, 1988). As shown at Fig. 7A, the simulation of the aboveground phytomass dynamics of this ecosystem by the CENTURY model is nearly perfect: $D_{abs} = 13.9$ g/m^2 (8.1% of G_{max}). The representation of the dynamics of the aboveground mortmass here is also quite satisfactory (Fig. 7B), though in this latter case it is more natural to speak about correct simulation of the general trend

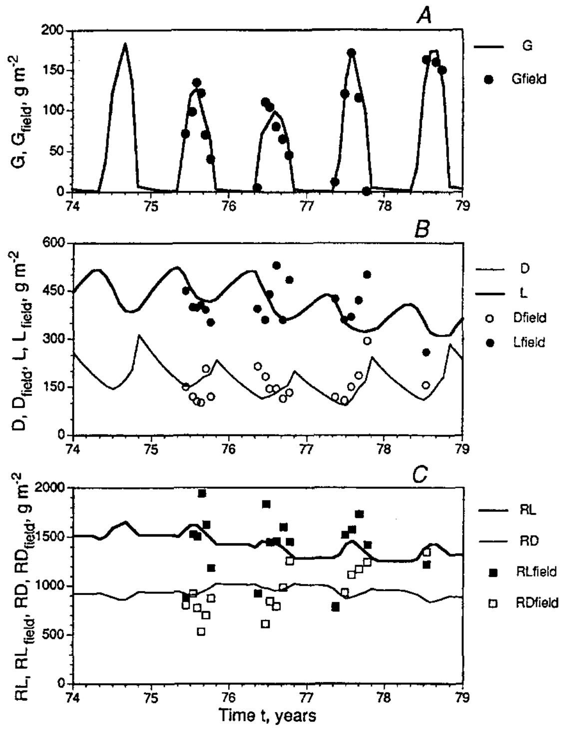

Fig. 7. Dynamics of the aboveground live phytomass G (g m^{-2}) (A), $D_{abs} = 13.9$ g m^{-2}, aboveground mortmass (= standing dead D plus litter L) (B), and the live belowground phytomass RL and dead belowground phytomass RD (C) in the dry continental steppe ecosystem of the Shortandy site for the 1975–1979 period. Points – field data after Shatokhina (1988); curve – simulation results using the real meteorological data for the same period.

and limits of variability than about a detailed point-to-point correspondence, observed for the live aboveground phytomass. The good performance of the CENTURY model on this data set is partly due to the fact that the natural conditions of the dry steppe at the Shortandy site are very similar to the short-grass prairie of Colorado, for which the model was initially developed.

An important feature of the productivity investigation at the Shortandy site is the emphasis on the quantitative study of the dynamics and production of the belowground phytomass, which was accomplished according to the repeated soil monolith sampling method by Titlyanova (1977), modified by Shatokhina (1980, Shatokhina, 1988). The field data on live (RL) and dead (RD) belowground phytomass dynamics at the Shortandy dry continental steppe are presented at Fig. 7C along with the modeling results. As was pointed out by Singh et al. (1984), the field measurements of the belowground phytomass in grasslands are characterized by high variability (CV > 30%). This should be taken into account while comparing the field and model belowground data. With this in mind, we came to the conclusion that the CENTURY model not only successfully calculates the average amounts of live and dead phytomass of the dry steppe community, but is also capable to depict its characteristic seasonal dynamics, especially the late summer peak on the live root phytomass curve RL, which is considered to be a peculiarity of the seasonal carbon cycle of the non-tropical grasslands (Titlyanova, 1977). The slope of regression at the scatter diagram for the Shortandy site is 0.98 and the r^2 is 0.98. The results indicate a close agreement between the empirical data and the model outputs for the dry continental steppe ecosystem.

6.5. Dzhanybek – DZH

The Dzhanybek research station, representing the semidesert grassland on the chestnut soil, also has a uniquely long time series of phytomass observations (Fig. 8): for the period from 1955 to 1984 (excluding 1976) the peak phytomass data G_{max} were collected (Gordeeva and Larin, 1965; Olovyannikova, 1976; Olovyannikova, personal communication), and during the 1985–1989 period more detailed data on the seasonal dynamics of both live and dead aboveground phytomass were obtained (Gilmanov and Ivaschenko, 1990).

Except of the failure in the 1959 (cf. Fig. 8), the agreement between the field data and the model seems satisfactory. For the whole data set of $n = 61$ points the error $D_{abs} = 36.2$ g/m^2 or 16.5% of G_{max}; the slope of the regression line on the scatter diagram is $b = 0.88$, while $R^2 = 0.85$. This semidesert ecosystem is noted by its highly irregular pattern of precipitation so that the model dynamics represents the sequences of interchanging 'good' and 'bad' years. Despite certain discrepancies within some seasons (due to seasonal lags brought about by the monthly time step), the model successfully predicts the maximum phytomass values for each year. The mean absolute error of maxima prediction is equal to

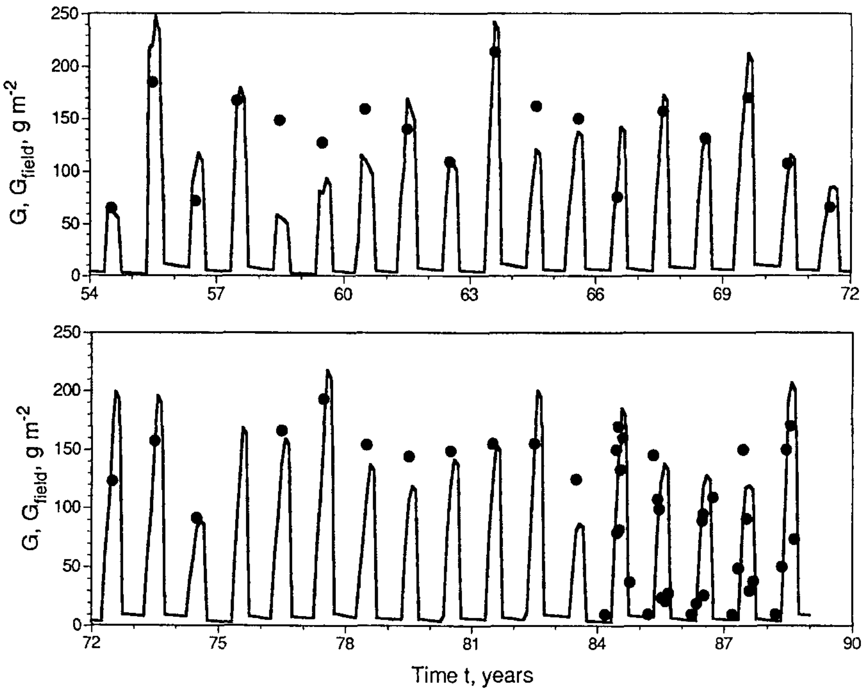

Fig. 8. The long-term dynamics of the aboveground live phytomass G (g m^{-2}) in the semidesert grassland ecosystem of the Dzhanybek site during the 1954–1989 period. Points – field data after Gordeeva and Larin (1965), Olovyannikova (1976; personal communication), Gilmanov and Ivaschenko (1990); curve – simulation results using the real meteorological data for the same period (D_{abs} = 36.2 g m^{-2}).

$D_{abs}(\max) = 26.2$ g/m^2 (10.8% of G_{max}), while the regression slope $b(\max)$ is 0.99, and $R^2 = 0.95$.

On the other hand, in some years notable deviations of the model from the data occur within the season. For instance, in 1986 the model was unable to generate the large early spring peak of production with subsequent dying off at the first half of the summer; in 1987 a secondary autumn growth of

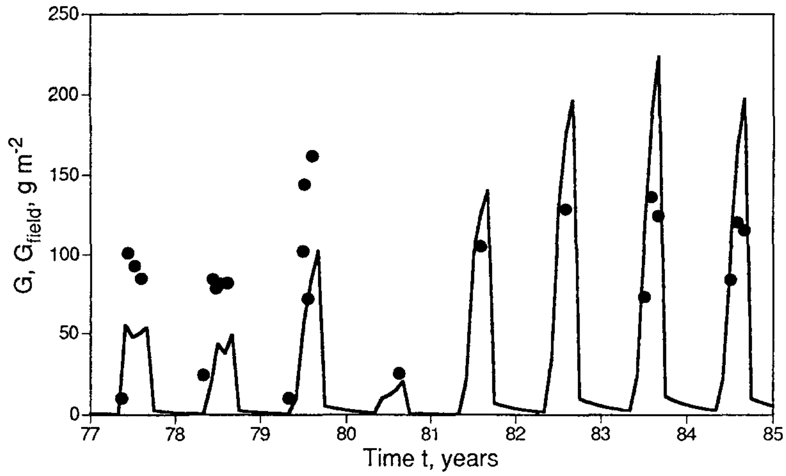

Fig. 9. The long-term dynamics of the aboveground live phytomass G (g m^{-2}) in the ultracontinental cryoarid grassland ecosystem of the Tuva site during the 1979–1985 period. Points – field data after Gorshkova (Gorshkova, 1982; Gorshkova, 1986); curve – simulation results using the real meteorological data for the same period (D_{abs} = 49.4 g m^{-2}).

phytomass to more than 100 g/m^2 had taken place, but was not simulated by the model.

6.6. Tuva – TUVA

The CENTURY model dynamics at the ultracontinental steppe of the Tuva site is of particular interest, because the climatic, physiognomic and bionomic properties of this cryoarid ecosystem are considerably different from those of the grasslands of North American Great Plains, for which the model parameters were identified originally. As can be seen from Fig. 9, despite all the differences mentioned, the model proved to be an efficient tool to simulate the performance of the cryoarid steppe ecosystem at the year-to-year level, i.e., with respect to the response of the aboveground phytomass to the weather conditions of a given year, whether it is a 'bad' year (1981), a 'moderate' year (1978, 1979 and 1982), or a 'good' year (1983–1985). Within the particular growing season the differences between the model and observations may be substantial, but without definite bias to the negative or the positive side (cf. years 1980 and 1984). The seasonal differences reflect the sensitivity of certain grassland systems to episodic rainfall events that cannot be resolved with the monthly time step model. The poorer agreement between the data and the model for this ecosystem compared to those described above is illustrated by the slope of the scatter diagram $b = 0.84$ which is less then 1.0 and the lower value $R^2 = 0.77$.

6.7. Badkhyz – BAD

The physico-geographical conditions and bionomical properties of the desert grassland ephemeretum of the Badkhyz site are also appreciably different from the classic steppes and prairies, making this validation site an important test to determine the limits of applicability of the CENTURY model. The time series of observations at the Badkhyz site is sufficiently long, encompassing 30 years (1948–1972, 1977–1982) with high variability of weather regimes – from the most unfavorable year 1948 to

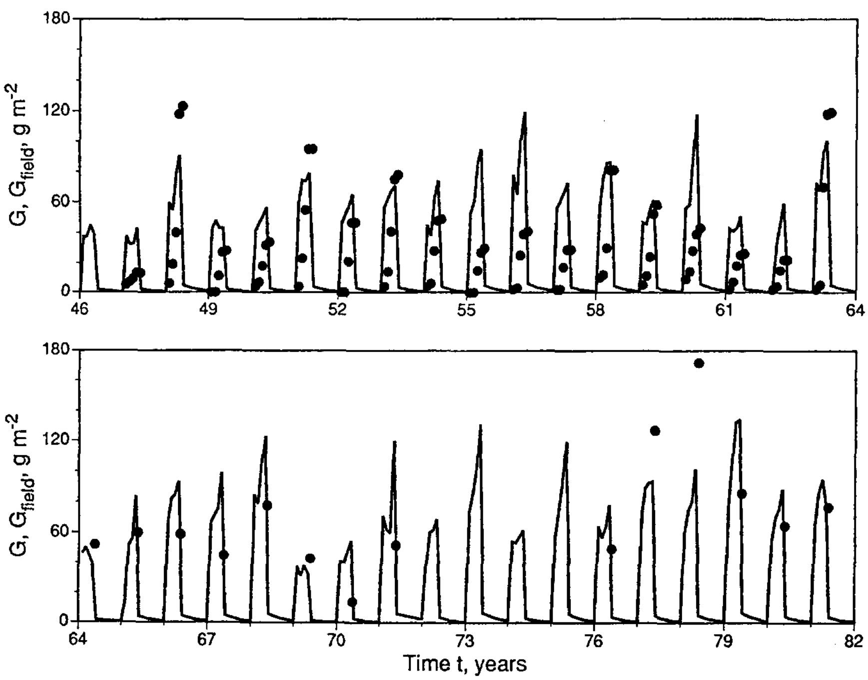

Fig. 10. The long-term dynamics of the aboveground live phytomass G (g m^{-2}) in the serozem desert grassland ecosystem of the Badkhyz site during the 1946–1982 period. Points – field data after Nechaeva et al. (1971), Artykov (1975), and Gannibal (1986); curve – simulation results using the real meteorological data for the same period ($D_{abs} = 38.6$ g m^{-2}).

the most favorable year 1978 (Fig. 10). The distinguishing features of the climate of the serozem desert grassland ephemeretum include (i) an early and short growing season (February to April/May), (ii) a considerable but irregular role of spring ephemerals in the phytomass production of the community, and (iii) the ephemeral-like (= ephemeroidal) phenology of principal perennial species, such as dominants *Poa bulboasa* and *Carex pachystylis*.

In view of the comments above and considering the validation of the CENTURY model on the Badkhyz data set (Fig. 10) one can not deny that even in this extreme case the agreement between the field data and the model is not as bad as might be expected. First of all, this site confirms the statement that the general regularities of the influence of the hydro-thermal factors and nitrogen regime, lying in the basis of the CENTURY model, are to a great extent valid in this case also. The mean absolute deviation between the data and model was found to be $D_{abs} = 38.6$ g/m^2 (22.5% of G_{max}).

A certain inadequacy of the model on the Badkhyz data set is revealed at the scatter diagram of observed versus simulated phytomass data, where the regression slope (b) is 0.58 and deviated the most from 1.0. The low R^2 value of 0.41 indicates high scattering. But under more thorough examination one comes to the conclusion that the major part of this variability is caused by the intraseasonal deviations of the simulation results to the observed the data, related to the unmatched description of the course of phenological development in different years. Meanwhile, the general pattern of the year-to-year dynamics of the phytomass, expressed by the correspondence of the field (empirical) and model maxima, is represented by the model rather reasonably: at the scatter diagram of G_{max}(data) versus G_{max}(model) the slope $b = 0.88$ and $R^2 = 0.64$.

7. Model performance across the gradient

Assessment of the CENTURY model for the different types of grassland ecosystems of the former USSR are summarized in Table 5. Here the model performance for all eight tested ecosystems is characterized by parameters $D_{abs,\%}$, b and r^2 simultaneously, where $D_{abs,\%}$ is the mean error of simulation, expressed as a percentage of the corresponding phytomass maximum G_{max}, and b is the slope of the regression on the scatter diagram of empirical versus model phytomass maximum values. The best correspondence between the field data and the model is observed for the dry steppe of the Shortandy site, where the mean simulation error is near 8% and the slope of the regression on the scatter diagram is very near to 1.0. The least satisfactory are the results of modeling aboveground phytomass dynamics at the ultracontinental cryoarid steppe of the Tuva and the serozem desert steppe of the Badkhyz. The moderate upland meadows of the Otradnoye site, the typical steppe of the Khomutov site and the semidesert steppe of the Dzhanybek site performed satisfactorily.

Thus, the data obtained lead us to the conclusion that CENTURY has a reasonably good potential to reproduce the seasonal, mid-term and in some cases the long-term dynamics of the live and dead aboveground phytomass of the grassland ecosystems in highly different natural-climatic zones of the former

Table 5
Performance indexes of the CENTURY model for selected grassland sites of the former USSR

Code	Site	Mean absolute difference D_{abs} (% of G_{max})	Regression slope b (g/g)	Correlation coefficient r^2
OTRL	Otradnoe loamy meadow	10.8	0.98	0.67
OTRS	Otradnow sandy meadow	13.2	0.95	0.58
KURSK	Kursk meadow steppe	17.3	0.91	0.67
KHOM	Khomutov typical steppe	20.8	0.88	0.80
SHOR	Shortandy dry steppe	8.1	0.98	0.98
DZH	Dzhanybek semidesert steppe	16.5	0.88	0.85
TUVA	Tuva dry ultracontinental steppe	27.1	0.84	0.77
BAD	Badkhyz desert grassland	22.5	0.88	0.64

USSR. The means and variation limits of the model are close to that of the field data. Limitation of CENTURY simulating seasonal dynamics of grassland productivity in the drier steppes represented reflect the difficulty of a monthly time-step model to capture the rapid response of grasses to intermittent rainfall which triggers growth in these ecosystems. The peak biomass and average dynamics of these ecosystems are adequately captured indicating that CENTURY does represent the general regularities of the influence of the hydrothermal factors and nitrogen nutrition on ecosystem productivity.

Further improvement of the model needs to proceed with a more detailed representation of phenological development and an introduction to the model of the possibility to explicitly describe the environmental response of several functionally, morphologically and taxonomically different groups of plants.

8. Climate / productivity relationships for Eurasian grasslands

Fig. 11 shows the comparison of CENTURY simulated and observed average aboveground net primary production estimates for grassland ecosystems of the former USSR. There is a definite positive correlation between predicted and observed data ($r^2 = 0.94$), but the model systematically underestimates observed production. However, interpreting the empirical ANPP estimates it is necessary to take into account that they were obtained using the minimum estimate method by Titlyanova (1977). This method calculates ANPP by utilizing the data of repeated harvesting of live phytomass, standing dead and litter during the growing season. As was pointed out by Singh et al. (1984), with insufficient replication in the field (which very often is the case in practice) the estimates provided by this calculation procedure are subjected to large errors. In any case, we see that CENTURY is successful enough in representing the general pattern of the ANPP trend along the Eurasian grassland gradient under study. The observed ANPP data were also compared with the ANPP regression equation from the Milchunas and Lauenroth (1993) paper (see Fig. 11) and shows that the r^2 is lower than that of CENTURY model results and the estimates of ANPP are approximately 50% of the observed data. This suggests that the production per cm

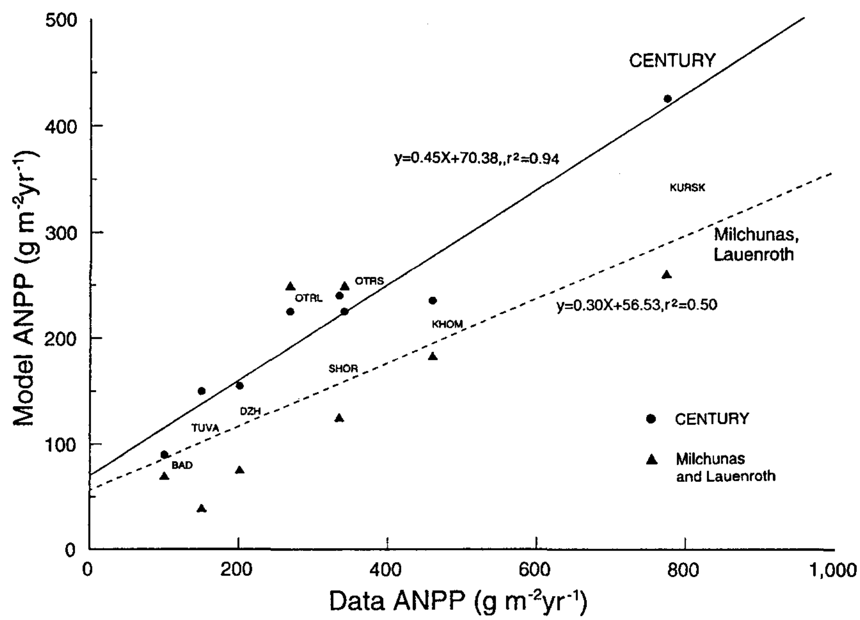

Fig. 11. Scatter diagram of CENTURY model ANPP predictions versus empirical ANPP estimates for various grassland ecosystems of the former USSR and the Milchunas and Lauenroth (1993) model versus the USSR ANPP data.

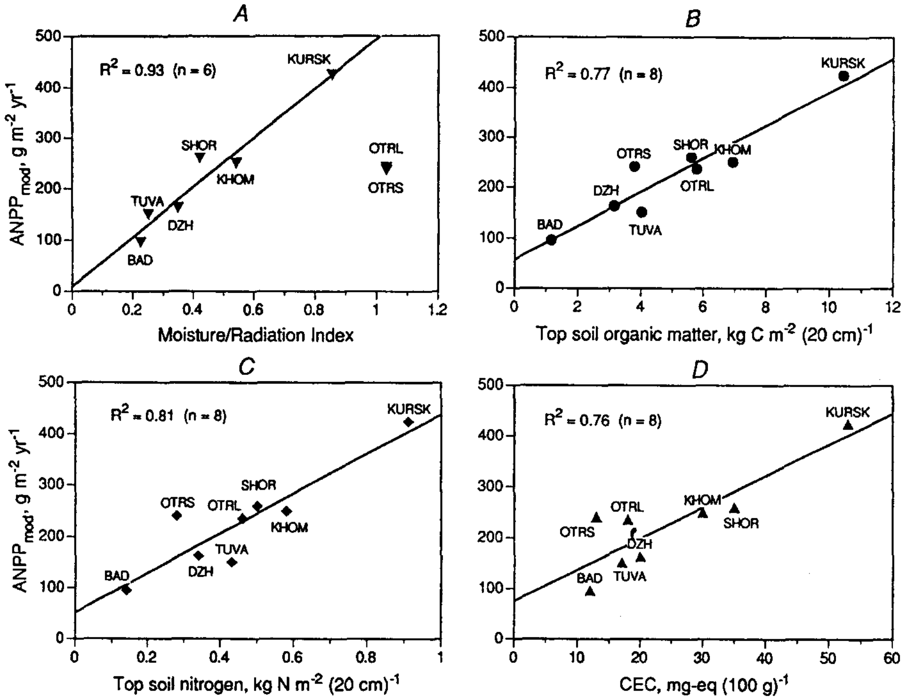

Fig. 12. Aboveground net primary production (ANPP, g m^{-2} yr^{-1}) of selected grassland ecosystems of the former USSR predicted by the CENTURY model in relation to leading fertility factors: (A) the moisture/radiation index ($P * L/R_b$); (B) soil organic matter (kg C m^{-2} 20 cm^{-1}); (C) total soil nitrogen (kg N m^{-2} 20 cm^{-1}); (D) cation exchange capacity (meq./100 g soil).

of precipitation is higher for Russian grasslands compared to other grasslands around the world.

The capability of the model to adequately describe the dependence of grassland productivity on leading climatic and soil fertility factors is illustrated in Fig. 12. The simulated ANPP values are plotted against MRI $= (P * L)/R_b$ (Fig. 12A), proposed by Grigoryev and Budyko (1956). As can be seen, for the conditions of insufficient moisture (MRI < 1) the model clearly demonstrates the same trend of linear relationship between ANPP and moisture conditions as documented by Sala et al. (1988) and Milchunas and Lauenroth (1993). Deviation of the forest-zone meadow sites OTRL and OTRS, for which the moisture/radiation index is greater than 1, can be explained by evaluating the soil chemistry and nutrient limitations at this site. The CENTURY model simulates the expected trends of variation of grassland productivity with main soil fertility characteristics: the monotoni increase with soil organic matter, nitrogen and cation exchange capacity (Fig. 12B–D). In Fig. 12B–D the points for forest zone meadows Otradnoe on soddy-podzolic soils lie in the lower end of the productivity range reflecting their poorer humus and nitrogen content and low cation exchange

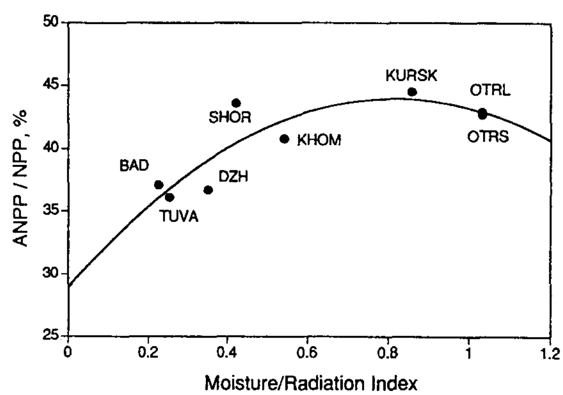

Fig. 13. Simulation by the CENTURY model of the pattern of the relationship between the ratio of aboveground to total net primary production (ANPP/NPP, %) and the moisture/radiation index ($P * L/R_b$) over the selected gradient of grassland ecosystems of the former USSR. The points denote CENTURY modeling results, the curve shows the overall trend.

capacity. This may provide an explanation of the deviation of the Otradnoe sites from the linear trend in Fig. 12A.

An important feature related to C dynamics in grassland ecosystems is the partitioning of C to above or belowground compartments. The observed trend in aboveground-to-belowground production partitioning (Miroshnichenko, 1975; Titlyanova, 1977; Shatokhina, 1988) relative to the MRI is depicted in Fig. 13. The CENTURY simulation from the eight grassland sites indicates that the model allowed greater belowground C allocation for sites with a MRI value of 0.4; as the MRI increased to values greater than 0.5, the allocation of C to aboveground increased to about 40 to 45% of total NPP.

9. Conclusion

Thus, the data obtained lead us to the conclusion, that the CENTURY model reproduces the seasonal, mid-term and in some cases the long-term dynamics of the live and dead aboveground phytomass of the grassland ecosystems in highly different natural-climatic zones of the former USSR. The means and variation limits of the model are close to that of the field data. The limit of applicability of the CENTURY model (CENTURY, version 3.1) extends to the extreme continentality gradient of the Eurasian continent, including the ephemero-ephemeroidal desert grasslands and ultracontinental cryoarid steppes. The CENTURY model is capable of simulating substantial features of seasonal and long-term dynamics of these ecosystems. As for further improvements of the model, we recommend: (i) more detailed representation of phenological development; (ii) introduction to the model of the possibility to explicitly describe the environmental response of the various functionally, morphologically and taxonomically different groups of plants.

Acknowledgements

Analysis of data from the sites in the former USSR was carried out under the Russian State Scientific and Technical Program No. 18 "Changes of the Natural Environment and Climate". Data synthesis and model validation was made possible by the SCOPE (Scientific committee on problems of the environment) Project "Effects of Climate Change on Production and Decomposition in Coniferous Forests and Grasslands (1989–1992)". Model development was primarily funded by the U.S. National Science Foundation (NSF) project BSR 9013888 "Coupling Ecosystem Processes and Vegetation Patterns Across Environmental Gradients", the U.S. NASA Earth Observing System project NACW-2662 "Using Multi-Sensor Data to Model Factors Limiting Carbon Balance in Global Grasslands", and the U.S. NSF project BSR 9011659 "Long term Ecological Research Program: Shortgrass Steppe".

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