Biology Bulletin, Vol. 28, No. 3, 2001, pp. 293–300. Translated from Izvestiya Akademii Nauk, Seriya Biologicheskaya, No. 3, 2001, pp. 353–361.
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ECOLOGY

Modeling the Values of Net Primary Production for the Zonal Vegetation of European Russia

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Received August 6, 1999

Abstract—Several modern approaches to the problem of estimating the net primary production of terrestrial ecosystems are discussed. A method for predicting the dynamics of this parameter as a function of radiation balance and annual evapotranspiration is described. The values of annual carbon by the zonal vegetation of European Russia are calculated in two ways: by methods based on the empirically determined relationships between the annual average values of climatic parameters and net primary production and on the basis of models describing carbon flows between the compartments of ecosystems. The model estimations of net primary production are compared with experimental data.

INTRODUCTION

Modeling the net primary production of terrestrial ecosystems is among the key problems in studies dealing with the effects of the anthropogenic impact on the quantitative parameters of global organic matter cycle and the structure of the biosphere as a whole. Net primary production, one of the key characteristics of the plant cover, is determined as the amount of organic matter accumulated in both above- and underground spheres of a plant community per unit of its area during a certain period of time (usually, a year). This parameter is calculated in units of organic matter dry weight and is usually expressed in carbon units, which show the content of carbon in dry organic matter. The concept of net primary production (*NPP*) was formulated by Bliss (1962), and this term became internationally accepted. It should be noted, however, that some specialists use other terms, such as "primary biological productivity," "annual increment," and "net annual production" of the vegetation, but their meaning is the same.

Changes in the spatial distribution of terrestrial *NPP* have a significant effect on the maintenance of homeostasis in the atmosphere, as *NPP* values characterize the annual rate of atmospheric carbon dioxide consumption by the terrestrial biota. Estimating the global and local values of *NPP* is an urgent problem in studies on both the biological cycle of organic matter in general and carbon cycle in the biosphere in particular.

To date, specialists have developed several dozen ecosystems and biosphere models that make it possible to estimate *NPP* for different zonal types of the vegetation. These models fall into two categories: bioclimatic (regression-based) (McGuire *et al.*, 1992), and ecophysiological (process-based). The first category comprises the models based on empirically determined relationships between the annual average values of climatic parameters and *NPP* values (Table 1). They make it possible to follow the annual dynamics of *NPP* in the plant cover. The models of the second category are based on the description of carbon flows (in some cases, together with nitrogen and water flows) between the atmosphere and different compartments of the plant cover and the soil. *NPP* in these models depends on several processes, including photosynthesis and plant respiration, evapotranspiration, organic matter dying off and decomposition (Table 2). Depending on the method used for parameterizing the processes considered, models of this type have different characteristic times and allow researchers to follow the seasonal dynamics of *NPP* in the plant cover of an ecosystem.

In this paper, we discuss different approaches to the assessment of annual carbon accumulation by the plant cover. For the ecosystems of European Russia, *NPP* values estimated by different methods are compared with its actual values observed in experiments.

METHODS FOR CALCULATING NET PRIMARY PRODUCTION

NPP can be estimated by various experimental methods, such as gasometry performed in different periods, with the results of measurements used in calculations taking into account seasonal and diurnal factors; aerodynamic measurements of vertical gradients of carbon dioxide concentrations in cenoses; determinations of final phytomass; and the chlorophyll method based on determinations of chlorophyll content per unit of phytocenosis area. However, direct *NPP* determination by empirical methods involves some difficulties because of plant cover heterogeneity, the subjectiveness of estimations at some stages of analysis, and standard errors of measurements. In addition, problems arise when the data of field observations (i.e., local

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Table 1. Bioclimatic (regression-based) models included in analysis

Model	Climatic parameters determining *NPP* values	References
Miami	annual precipitation, annual average air temperature	Lieth, 1975
Efimova's	radiation balance, radiation index of dryness	Efimova, 1977
Zubenok's	radiation balance, index of dryness	Zubenok, 1971
Varlygin–Bazilevich's	radiation balance, total evaporation	Varlygin and Bazilevich, 1992

Table 2. Ecophysiological (process-based) models included in analysis and corresponding methods for calculating *NPP*

Model	Method for calculating *NPP*	Characteristic time	References
CASA	$NPP = f(PAR, FRAR, T, AET/PET)$	one month	Potter *et al*., 1993;
(Carnegie Ames Stanford Approach model)			Field *et al*., 1995
CENTURY	$NPP = f(C_v, T, W, P, PET, N, P_f, S)$	"	Patton *et al*., 1993;
(General ecosystem level model)			Patton *et al*., 1995
TSUBIMO	$NPP = f(GPP)$	"	Alexandrov, Oikawa, 1997;
(Tsukuda Biosphere Model)	$GPP = f(D, G, k, T, P, r, I_0, K, LAI)$		Alexandrov *et al*., 1999
TEM	$NPP = GPP - R_A$	"	Raich *et al*., 1991;
(Terrestrial Ecosystem Model)	$GPP = f(C_{max}, PAR, LEAF, T, CO_2, W, N)$		McGuire *et al*., 1992;
	$R_A = f(GPP, T, C_v)$		Pan *et al*., 1996
FBM	$NPP = GPP - R_A$	one day	Ludeke *et al*., 1994;
(Frankfurt Biosphere model)	$GPP = f(PAR, LAI, T, W, CO_2)$		Kohlmaier *et al*., 1997
	$R_A = f(T, C_v)$		
SILVAN	$NPP = GPP - R_A$	six days	Kaduk, Heimann, 1996
(Simulating Land Vegetation and NPP model)	$GPP = f(PAR, LAI, T, CO_2, AET/PET)$		
	$R_A = f(T, C_v)$		

Note: (C_v) carbon concentration in the vegetation; (C_{max}) maximum rate of photosynthesis; (CO_2) atmospheric carbon dioxide concentration; (*PAR*) photosynthetically active radiation; (*P*) amount of precipitation; (*W*) soil moistening; (*PET*) potential evapotranspiration; (*AET*) actual evapotranspiration; (*FPAR*) absorbed photosynthetically active radiation; (*N*) inorganic nitrogen, (P_f) phosphorus, and (*S*) sulfur concentrations in the soil; (*D*) average daylight period in the growing season; (*G*) duration of the growing season; (*k*) conversion constant; (*r*) coefficient of light curve; (I_0) midday illumination intensity; (*K*) light attenuation factor; (*LAI*) relative area of leaves; (*LEAF*) the ratio of actual and maximally possible areas of leaves; and (*T*) air temperature.

measurements) are extrapolated in order to make some spatial generalizations.

The initial global *NPP* estimations for terrestrial ecosystems, made by extrapolating scarce empirical data, varied between 11 and 25 Gt C per year (see Kobak, 1988). Subsequently, experimental research provided new data on *NPP* in various plant communities and entire ecosystems. On this basis, *NPP* of the continental plant cover was estimated at 49–77 Gt C per year (Whittaker and Woodwell, 1969; Bazilevich *et al.*, 1970).

The work on generalizing the empirical estimations of terrestrial *NPP* promoted the development of a new approach to its measurement, which consists of determining the dependence of annual plant production on various climatic factors. Studies by Grigor'ev and Budyko (1956, 1962) were basic in this respect. These authors analyzed the relationship of geographic zoning with the parameters of heat supply (radiation balance) and moistening (radiation index of dryness). The latter index was determined as the ratio of annual radiation balance R (kcal/cm^2) to the amount of heat necessary for evaporating the annual amount of precipitation, LP; here, L is specific heat of evaporation (kcal/g), and P is annual precipitation (g/cm^2). The results of the analysis allowed these authors to formulate the concept that each gradation of moistening and radiation balance is characterized by a certain value of *NPP* of the plant cover as well as by a specific type of zonal vegetation. Elaborating this approach, Budyko and Efimova (1968) revealed the dependence of *NPP* of the natural plant cover on the annual sums of radiation balance and radiation index of dryness. According to these authors, plant *NPP* in each thermal belt reaches a peak when the

radiation index of dryness has a certain optimal value, which ranges from 0.8 to 1.0.

The use of more extensive empirical data on *NPP* allowed Efimova (1977) to determine more accurately its functional dependence on radiation balance and index of dryness in the main zonal plant formations of the world and to make a map of *NPP* in the restored plant cover of terrestrial ecosystems. According to the results of this study, *NPP* reaches a peak when the radiation index of dryness has values ranging from 0.5 to 1.0.

Varlygin and Bazilevich (1992) studied the dependence of *NPP* (t/ha/year) on the annual radiation balance R (GJ/m^2) and total evaporation E (mm per year) in the main zonal plant formations of the world. The results showed that annual evaporation in the regions with optimal conditions for plant production in all thermal belts varies in a wide range, from 50 mm in the polar belt to almost 1300 mm in the equatorial belt. Moreover, as the radiation balance increases, the range between the highest and lowest values of annual evaporation in plant formations of the corresponding regions broadens: in the polar belt, it does not exceed 50–100 mm; in the boreal belt, 100–200 mm; in the subboreal belt, it narrows to approximately 100 mm; in the subtropical belt, it broadens again to 100–250 mm; and in the tropical zone, including the equatorial belt, it reaches 200–250 mm.

Zubenok (1971) analyzed annual *NPP* (t/ha) as a function of radiation balance R (kcal/cm^2 per year) and the index of dryness E_0/P, which depends on annual values of evaporation E_0 (cm) and precipitation P (cm). The results showed that *NPP* of the plant cover under the same conditions of moistening (at constant E_0/P) increases with an increase in the radiation balance. Under insufficient moistening (at higher E_0/P), *NPP* decreases. High *NPP* values (above 22.5 t/ha per year) are observed at E_0/P varying within a fairly wide range, from 0.3 to 2.0 (Zubenok, 1976).

Lieth (1975) correlated the data on annual *NPP* (kg/m^2) in various terrestrial ecosystems with climatic data, such as annual precipitation P (mm) and annual average air temperature T (°C), and, on this basis, proposed the following formula for calculating *NPP*:

$$NPP = A\min\{1 - e^{-aP}, 1/(1 + ce^{-bT})\},$$

where $A = 1.46$, $a = 0.000664$, $b = 0.119$, and $c = 3.73$. This is one of the simplest methods for estimating *NPP* by climatic parameters, known as the Miami model. This model has been widely used in studies dealing with interactions in the vegetation–atmosphere system at both global and regional levels (see Esser, 1987, 1991; Belotelov *et al.*, 1996; Brovkin *et al.*, 1998; Jiang *et al.*, 1999).

The methods discussed above are based on empirically determined relationships between annual average values of climatic parameters and *NPP* and belong to the group of bioclimatic (regression-based) models. In the modern ecosystem and biosphere models that comprise the ecophysiological (process-based) group, two basic approaches to calculating *NPP* are used. In some models of this type, *NPP* is directly determined as a function of physiological characteristics of plants (absorption of photosynthetically active radiation, carbon assimilation, transpiration rate, etc.) and environmental parameters (precipitation, air temperature, soil moistening, the amount of accessible nitrogen in the soil, etc.). In particular, this concerns the CASA, CENTURY, and TSUBIMO models (Table 2). In some other models (e.g., TEM, FBM, and SILVAN), *NPP* is calculated as the difference between gross primary production (*GPP*), which determines the rate of carbon dioxide transformation into organic matter by photosynthesizing plants, and the amount of organic matter expended by autotrophic organisms for respiration (autotrophic respiration R_A):

$$NPP = GPP - R_A.$$

R_A is usually regarded as a function of air temperature and carbon concentration in the vegetation, and *GPP* is regarded as a function of photosynthetically active radiation intensity, soil moistening, air dryness, air and soil temperatures, carbon dioxide and oxygen concentrations in the atmosphere, species-specific features of plants, and soil types. Thus, ecophysiological models provide a more or less accurate description of complex relationships between the processes of organic matter turnover in ecosystems. However, the use of numerous parameters in models of this type created a situation in which not only a great amount of experimental information, but also numerous data obtained by modeling are necessary for their identification.

The results of modeling make it possible to estimate the global annual value of terrestrial *NPP* more accurately (Table 3). According to generalized experimental data, the global *NPP* of terrestrial ecosystems is 77.4 Gt C per year (Bazilevich *et al.*, 1970). The values calculated according to various models range from 46.6 to 61.6 Gt C per year. The greatest value was obtained using the TSUBIMO model, in which *NPP* of the plant cover is calculated on the basis of radiation

Table 3. Estimations of global terrestrial *NPP*

Model	*NPP*, Gt C per year	References
TSUBIMO	61.6	Alexandrov *et al*., 1999
SILVAN	61.1	Cramer *et al*., 1999
Efimova's	56.4	Efimova, 1977
CASA	56.4	Field *et al*., 1998
CENTURY	53.3	Cramer *et al*., 1999
TEM	53.2	Melillo *et al*., 1993
FBM	50.3	Kohlmaier *et al*., 1997
MIAM	46.6	Lieth, 1975

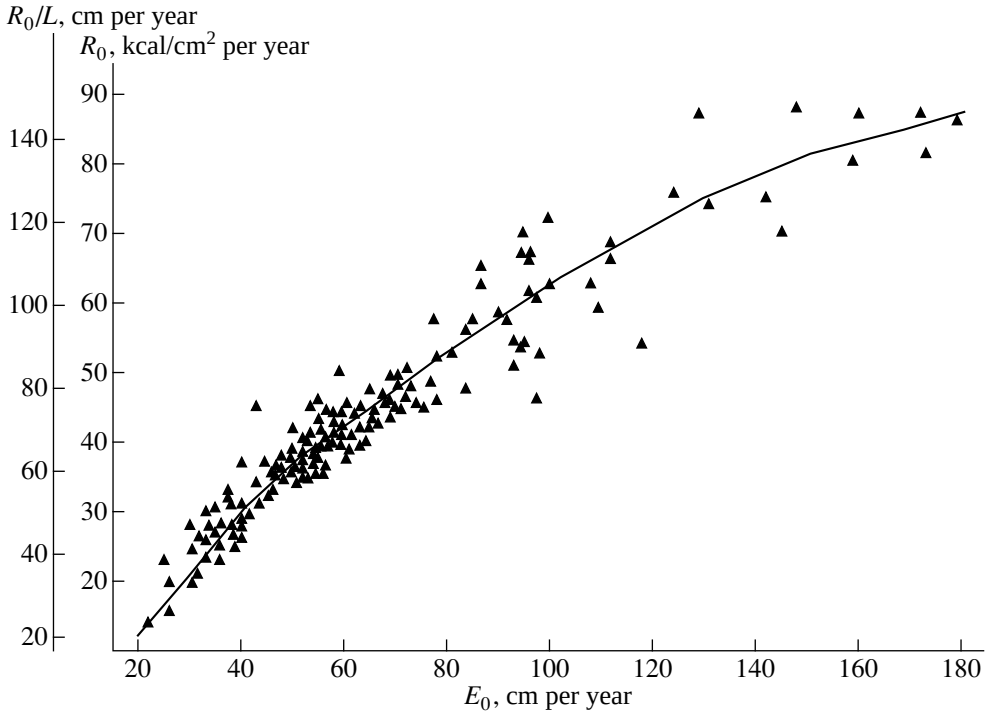


Fig. 1. Experimental data (according to Zubenok, 1976; triangles) and the plot (solid line) illustrating the dependence of radiation balance in a moistened area (R_0) and evaporativity calculated from radiation balance (R_0/L) on evaporativity determined by a complex method (E_0).

and heat parameters. The result of calculations by the SILVAN model, which takes into account water balance in addition to radiation and heat parameters, was 61.1 Gt C. Efimova's bioclimatic scheme and the CASA model gave a slightly smaller value (56.4 Gt C). According to the models based on nitrogen cycle (CENTURY and TEM), the annual value of terrestrial *NPP* is about 53 Gt C. The Frankfurt Biosphere Model (FBM), in which the processes of carbon and water transfer in the atmosphere–vegetation–soil system are parameterized, gave an estimate of 50.3 Gt C per year. Finally, the lowest value of *NPP* for terrestrial ecosystems—46.6 Gt C per year—was obtained using the MIAMI model.

RESULTS OF MODELING

The aforementioned methods for calculating *NPP* provide the possibility of estimating the spatial distribution of the resulting values of *NPP* in plant communities. Let us compare the results of modeling by each method with empirical data using the ecosystems of European Russia as an example. On the one hand, European Russia is heterogeneous with respect to both climatic conditions and the types of plant formations; on the other, there is a large database of empirically determined *NPP* values for this region compiled by Bazilevich (1993). For the purposes of our study, we used a spatial coordinate grid with a resolution of $0.5° \times 0.5°$ (geographic latitude by longitude). The

Table 4. Ranges of evaporation (E), evaporativity (E_0), radiation balance (R), index of dryness (E_0/P), and radiation index of dryness (R/LP) for natural zones of European Russia

Zone	E, cm per year	E_0, cm per year	R, GJ/m^2 per year	E_0/P	R/LP
Tundra	13.0–28.3	25.0–35.9	0.70–0.96	0.31–0.67	0.38–0.64
Coniferous forests	21.7–48.3	28.9–57.0	0.75–1.50	0.42–0.81	0.44–0.80
Mixed forests	37.0–55.5	48.1–60.1	1.18–1.64	0.60–0.95	0.66–0.96
Broadleaved forests	37.0–57.0	55.3–65.0	1.43–1.73	0.71–1.14	0.75–1.20
Meadow steppes	37.2–57.4	56.2–70.6	1.44–1.76	0.73–1.29	0.80–1.31
True steppes	35.0–63.3	58.2–100.7	1.52–2.22	0.84–2.52	0.97–2.11
Semideserts	25.0–60.0	72.4–101.2	1.69–2.14	1.53–3.35	1.42–2.80

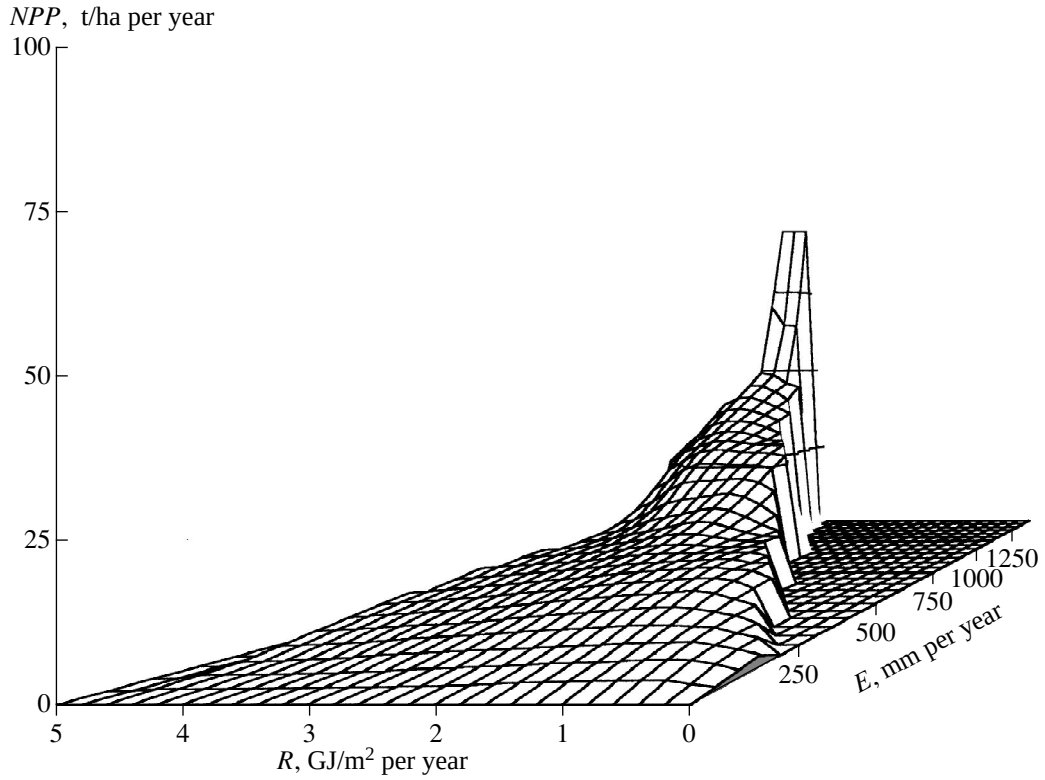


Fig. 2. A surface of *NPP* values depending on radiation balance *R* and total evaporation *E* (according to Varlygin and Bazilevich, 1992).

types of vegetation were determined using the vegetation map of the former Soviet Union (*Fiziko-geograficheskii atlas mira*, 1964) with corrections made by Bazilevich at the Institute of Geography, Russian Academy of Sciences. The sums of annual precipitation *P*, evaporation *E*, and evaporativity E_0 were taken from *Mirovoi vodnyi balans* … (1974); annual average air temperatures and radiation balance *R* were determined from the data presented in *Fiziko-geograficheskii atlas mira* (1964).

The dependence of the radiation balance R_0 on evaporativity E_0 in a moistened area, determined by a complex method, and the dependence of evaporativity calculated from radiation balance (R_0/L) on evaporativity E_0 were used to determine the values of the radiation index of dryness R/LP in the coordinate grid. The functional relationships between these parameters (Fig. 1) were revealed on the basis of experimental data described by Zubenok (1976).

The results of modeling showed that the main zonal plant formations in European Russia are distributed depending on the ranges of E, E_0, R, E_0/P, and R/LP values (Table 4).

Taking into account data on the average annual air temperature and precipitation in European Russia, we estimated *NPP* for the ecosystems of this region according to the Miami model. Data on the radiation balance and R/LP and E_0/P values allowed us to calculate *NPP* according to the models proposed by Efimova and Zubenok.

The nomogram describing the empirically determined relationships between *NPP* of zonal plant formations, on the one hand, and radiation balance *R* and total evaporation *E*, on the other (Varlygin and Bazilevich, 1992), and the method of piecewise-cubic interpolation (Marchuk, 1980) provided the basis for inventing an algorithm to calculate *NPP* depending on *R* and *E* values. The proposed method allowed us to present *NPP* as a continuous function of these two parameters. Its plot is shown in Fig. 2. The data on the radiation balance and total evaporation and the formal description of *NPP* as their function were used to calculate *NPP* values by Varlygin–Bazilevich's model.

To calculate *NPP* for the ecosystems of European Russia according to the CASA, CENTURY, and SILVAN models, we received their authors' permission to use the data obtained by specialists participating in the project "The Potsdam Net Primary Production Model Intercomparison," headed by Prof. W. Cramer (Potsdam Institute for Studies on Climate Change, Germany). The data for calculations by the FBM model were kindly supplied by Prof. M.K.B. Ludeke (Potsdam Institute for Studies on Climate Change); the

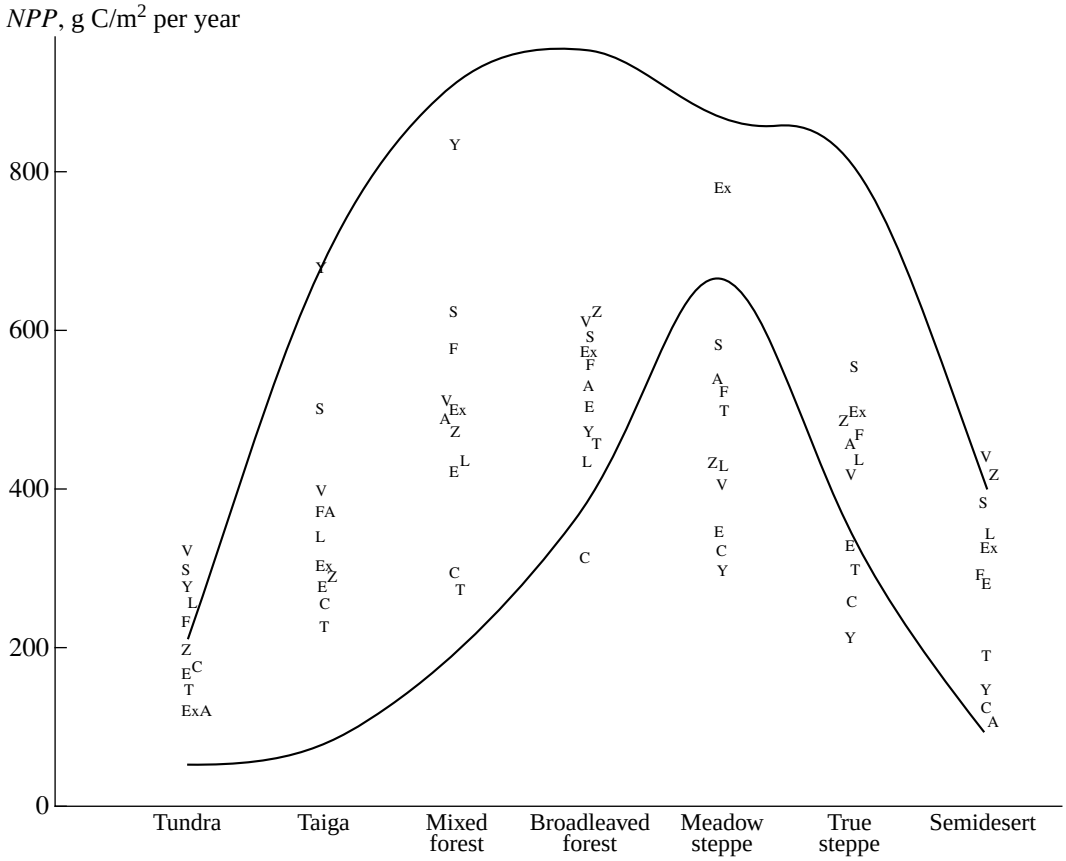


Fig. 3. Comparison of *NPP* values calculated according to (S) SILVAN, (Y) CENTURY, (F) FBM), (A) TSUBIMO, (T) TEM, (C) CASA, (L) MIAMI, (Z) Zubenok's, (V) Varlygin–Bazilevich's, and (E) Efimova's models with (Ex) experimental data on zonal ecosystems of European Russia (according to (B) Bazilevich, 1993). Lines show the limits of variation in experimentally determined *NPP* values.

TSUBIMO model was applied to the data received from G.A. Alexandrov, the author of this model (University of Tsukuba, Japan); and the TEM model, to the results published by Melillo *et al.* (1993).

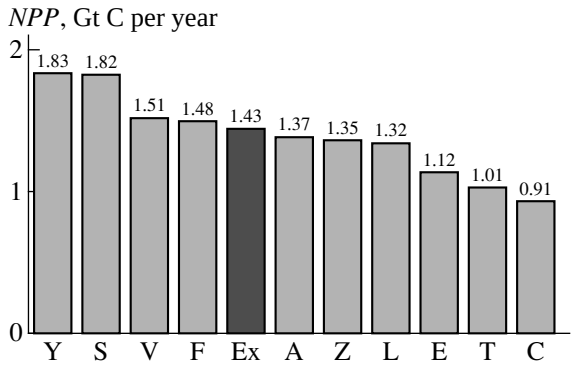


Fig. 4. Estimations of *NPP* for the plant cover of European Russia. For designations, see Fig. 3.

Figure 3 shows annual *NPP* values determined for the ecosystems of European Russia with the use of these models. *NPP* values determined experimentally and calculated by the methods proposed by Zubenok, Efimova, and Varlygin and Bazilevich were converted into carbon units using coefficients reported by Svirezhev *et al.* (1997).

CONCLUSION

In the case of tundra ecosystems, the results obtained with the use of Efimova's, Zubenok's, TSUBIMO, CASA, and TEM models proved to fall within the range of experimentally determined *NPP* values, whereas all other estimations exceeded these values. The results of calculations by the TSUBIMO and TEM models approached the actual *NPP* values most closely.

In the case of temperate forest ecosystems, virtually all calculated *NPP* values were within the range of experimentally determined values, except for *NPP* of broadleaved forests estimated according to the CASA model. The results that closely approached the averaged experimentally determined *NPP* values were

obtained using the following models: in the taiga zone, Efimova's and Zubenok's models; in the mixed forest zone, Varlygin–Bazilevich's model; and in the broadleaved forest zone, FBM and SILVAN.

In the meadow steppes, experimentally determined *NPP* is greater than in the first two zones, and all the models proved to underestimate this parameter by a factor of 1.5–2. In the true steppes, *NPP* values calculated according to Zubenok's, Varlygin–Bazilevich's, TSUBIMO, Miami, FBM, and SILVAN models were within the range of values measured experimentally. However, only Zubenok's and FBM models yielded results that closely approached the actual average *NPP* values characteristic of this zone.

In the semidesert zone, *NPP* estimations were mostly within the range of experimentally determined values, except for those made with Zubenok's and Varlygin–Bazilevich's model. *NPP* estimated using the Miami model closely approached the average value determined for this zone experimentally.

These results show that correspondence between calculated and experimentally determined *NPP* values is closer in the zone of temperate forests; therefore, the models considered in this study are better adapted to the forest ecosystems of temperate latitudes.

The total annual *NPP* of all ecosystems is an important parameter of carbon cycle in the biosphere. According to experimental observations (Bazilevich, 1993), the plant cover of European Russia accumulates more than 1.43 Gt C per year. Model estimations of *NPP* for this region vary between 0.91 and 1.83 Gt C per year (Fig. 4). Compared to empirical data, the CASA model underestimates annual *NPP* by 36%, whereas the SILVAN and CENTURY models overestimate it by almost 28%. Closer correspondence between calculated and experimentally determined *NPP* values is observed in cases of the Frankfurt model (1.48 Gt C per year) and the TSUBIMO model (1.37 Gt C per year).

The analysis of annual *NPP* values determined for European Russia showed that the models employing numerous physiological and environmental parameters and the models based on the dependence of production on climatic factors produce comparable results. It should be noted that ecophysiological models give more variable *NPP* values (relative to expert estimations of this parameter) than bioclimatic models. Comparing the results of modeling, we revealed the models allowing *NPP* estimation for all the types of zonal vegetation characteristic of European Russia and ensuring a close approximation of experimentally determined *NPP* values. Our study showed that, in European Russia, possible trends in the dynamics of annual *NPP* upon climate change can be revealed with the aid of relatively simple models based on relationships between biological and climatic parameters.

ACKNOWLEDGMENTS

This study was supported by the Russian Foundation for Basic Research, project no. 99-05-65155.

REFERENCES

Alexandrov, G.A. and Oikawa, T., Contemporary Variations of Terrestrial Net Primary Production: The Use of Satellite Data in the Light of an Extremal Principle, *Ecol. Model.*, 1997, vol. 95, pp. 113–118.

Alexandrov, G.A., Yamagata, Y., and Oikawa, T., Towards a Model for Projecting Net Ecosystem Production of the World Forests, *Ecol. Model.*, 1999, vol. 123, pp. 183–191.

Bazilevich, N.I., *Biologicheskaya produktivnost' ekosistem Severnoi Evrasii* (Biological Productivity of Ecosystems in Northern Eurasia), Moscow: Nauka, 1993.

Bazilevich, N.I., Rodin, L.E., and Rozov, N.N., Geographic Aspects of Studies on Biological Productivity, in *Materialy V s"ezda Geograficheskogo obshchestva SSSR* (Proc. V Conf. of the Geographic Society of the Soviet Union), Leningrad: Gidrometeoizdat, 1970, pp. 1–28.

Belotelov, N., Bogatyrev, B., Kirilenko, A., and Venevsky, S., Modelling of Time-Dependent Biome Shifts under Global Climate Changes, *Ecol. Model.*, 1996, vol. 87, pp. 29–40.

Bliss, L.C., Net Primary Production of Tundra Ecosystem, in *Die Stoffproduktion der Pflanzendecke*, Stuttgart: Springer, 1962, pp. 72–84.

Brovkin, V., Claussen, M., Petoukhov, V., and Ganopolski, A., On the Stability of Atmosphere–Vegetation System in the Sahara/Sahel Region, *J. Geophys. Res.*, 1998, D24, vol. 31, pp. 613–631.

Budyko, M.I. and Efimova, N.A., Solar Energy Utilization by the Plant Cover on the Territory of the Soviet Union, *Bot. Zh.*, 1968, vol. 53, no. 10, pp. 1384–1389.

Cramer, W., Kicklighter, D.W., Bondaeu, A., *et al*., Comparing Global Models of Terrestrial Net Primary Productivity (*NPP*): Overview and Key Results, *Global Change Biol.*, 1999, vol. 5, pp. 1–15.

Efimova, N.A., *Radiatsionnye faktory produktivnosti rastitel'nogo pokrova* (Radiation Factors of Plant Cover Productivity), Leningrad: Gidrometeoizdat, 1977.

Esser, G., Sensitivity of Global Carbon Pools and Fluxes to Human and Potential Climatic Impacts, *Tellus*, 1987, 39B, vol. 3, pp. 245–260.

Esser, G., Osnabruck Biosphere Model: Structure, Construction, Results, in *Modern Ecology: Basic and Applied Aspects*, Esser, G. and Overdieck, D., Eds., Amsterdam: Elsevier, 1991, pp. 679–709.

Field, C.B., Randerson, J.T., and Malmstrom, C.M., Global Net Primary Production: Combining Ecology and Remote Sensing, *Remote Sens. Environ.*, 1995, vol. 51, pp. 74–88.

Field, C.B., Behrenfeld, M.J., Randerson, J.T., and Falkowsky, P., Primary Production of the Biosphere: Integrating Terrestrial and Oceanic Components, *Science*, 1998, vol. 281, pp. 237–240.

Fiziko-geograficheskii atlas mira (A Physiographic Atlas of the World), Moscow: GUGK, 1964.

Grigor'ev, A.A. and Budyko, M.I., On the Periodic Law of Geographic Zonality, *Dokl. Akad. Nauk SSSR*, 1956, vol. 110, no. 1, pp. 129–132.

Grigor'ev, A.A. and Budyko, M.I., On Seasonal Changes in the Climatic Factors of Geographic Zonality, *Dokl. Akad. Nauk SSSR*, 1962, vol. 143, no. 2, pp. 391–393.

Jiang, H., Apps, M.J., Zhang, Y., *et al*., Modeling the Spatial Pattern of Net Primary Productivity in Chinese Forests, *Ecol. Model.*, 1999, vol. 122, pp. 275–288.

Kaduk, J. and Heimann, M., A Prognostic Phenology Scheme for Global Terrestrial Carbon Cycle Models, *Clim. Res.*, 1996, vol. 6, pp. 1–19.

Kobak, K.I., *Bioticheskie komponenty uglerodnogo tsikla* (Biotic Components of Carbon Cycle), Leningrad: Gidrometeoizdat, 1988.

Kohlmaier, G.H., Badeck, F.-W., Otto, R.D., *et al*., Frankfurt Biosphere Model: A Global Process-Oriented Model for the Seasonal and Long-Term CO_2 Exchange between Terrestrial Ecosystems and the Atmosphere: 2. Global Results for Potential Vegetation in an Assumed Equilibrium State, *Clim. Res.*, 1997, vol. 8, pp. 61–87.

Lieth, H., Modeling the Primary Productivity of the World, in *Primary Productivity of the Biosphere*, Lieth, H. and Whittaker, R.H., Eds., New York: Springer, 1975, pp. 237–262.

Ludeke, M.K.B., Badeck, F.-W., Otto, R.D., *et al*., Frankfurt Biosphere Model: A Global Process-Oriented Model for the Seasonal and Long-Term CO_2 Exchange between Terrestrial Ecosystems and the Atmosphere: 1. Model Description and Illustrating Results for the Vegetation Types Cold Deciduous and Boreal Forests, *Clim. Res.*, 1994, vol. 4, pp. 143–166.

Marchuk, G.I. *Metody vychislitel'noi matematiki* (Methods of Calculus Mathematics), Moscow: Nauka, 1980.

McGuire, A.D., Melillo, J.N., Joyce, L.A., *et al*., Interactions between Carbon and Nitrogen Dynamics in Estimating Net Primary Productivity for Potential Vegetation in North America, *Global Biogeochem. Cycles*, 1992, vol. 6, no. 2, pp. 101–124.

Melillo, J.M., McGuire, A.D., Kicklighter, D.W., *et al*., Global Climate Change and Terrestrial Net Primary Production, *Nature*, 1993, vol. 363, pp. 234–240.

Mirovoi vodnyi balans i vodnye resursy Zemli (Global Water Balance and Water Resources of the Earth), Moscow: Gidrometeoizdat, 1974.

Pan, Y., McGuire, A.D., Kicklighter, D.W., and Melillo, J.M., The Importance of Climate and Soils for Estimates of Net Primary Production: A Sensitivity Analysis with the Terrestrial Ecosystem Model, *Global Change Biol.*, 1996, vol. 2, no. 1, pp. 5–23.

Parton, W.J., Scurlock, J.M.O., Ojima, D.S., *et al*., Observation and Modeling of Biomass and Soil Organic Matter Dynamics for the Grassland Biome Worldwide, *Global Biogeochem. Cycles*, 1993, vol. 7, pp. 785–809.

Parton, W.J. Ojima, D.S., and Schimel, D.S., Models to Evaluate Soil Organic Matter Storage and Dynamics, in *Structure and Organic Matter Storage in Agricultural Soils*, Carter, M.R. and Stewart, B.A., Eds., New York: Lewis, 1995, pp. 421–448.

Potter, C.S., Randerson, J.T., Field, C.B., *et al*., Terrestrial Ecosystem Production: A Process Model Based on Global Satellite and Surface Data, *Global Biogeochem. Cycles*, 1993, vol. 7, pp. 811–841.

Raich, J.W., Rastetter, E.B., Melillo, J.M., *et al*., Potential Net Primary Productivity in South America: Application of Global Model, *Ecol. Appl.*, 1991, vol. 1, pp. 399–429.

Svirezhev, Yu.M., Golubyatnikov, L.L., Denisenko, E.A., and Brovkin, V.A., A Model Approach to the Assessment of Total Exchange Carbon Flow for Ecosystems of European Russia, *Zh. Obshch. Biol.*, 1997, vol. 58, no. 2, pp. 5–14.

Varlygin, D.L. and Bazilevich, N.I., Relationships between Production of World Zonal Plant Formations and Some Climatic Parameters, *Izv. Ross. Akad. Nauk, Ser. Geogr.*, 1992, no. 1, pp. 23–32.

Whittaker, R.H. and Woodwell, G.M., *Measurement of Net Primary Production of Forests*, Brussels: Bookhaven Nat. Lab. Document 14056, 1969.

Zubenok, L.I., Climatic Factors and Plant Cover Productivity, *Tr. Gos. Geogr. O–va*, 1971, issue 287, pp. 90–95.

Zubenok, L.I., *Isparenie na kontinentakh* (Evaporation on Continents), Leningrad: Gidrometeoizdat, 1976.