

Aggregated Estimation of Basic Parameters of Biological Production and the Carbon Budget of Russian Terrestrial Ecosystems: 2. Net Primary Production

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The estimated net primary production (NPP) of Russian terrestrial ecosystems (annual average over the period from 1988 to 1992) is 9544 Tg of dry matter, or 4353 Tg of carbon. Of the total amount, forests account for approximately 39.2% (here and below, comparisons are made with respect to carbon content); natural grasslands and brushwoods, for 27.6%; farmlands (arable land and cultivated pastures), for 22.0%; and wetlands, for 11.2%. The average NPP density on lands covered with vegetation (1629.8 million hectares in Russia) is 267 g C/m² per year. The highest value (498 g C/m² per year) is characteristic of arable lands. Other land-use/land-cover (LULC) classes have the following NPP densities (in areas covered with vegetation): grasslands and brushwoods, 278 g C/m²; forests, 224 g C/m²; and wetlands, 219 g C/m² per year. In general, Russian terrestrial ecosystems accumulate 59.7% of the total NPP in the aboveground phytomass (47.8% in green parts and 11.9% in wood) and 40.3% in the underground phytomass. The latter parameter differs significantly in different LULC classes and bioclimatic zones. According to calculations, the uncertainty in estimating the total NPP is 11% (a priori confidential probability 0.9).

Key words: primary production, terrestrial ecosystems, carbon budget.

This paper is the second in a series devoted to the assessment of the carbon budget of Russian terrestrial ecosystems at the national level. Net primary production (NPP; below, sometimes referred to as production) is defined as the annual amount of plant organic matter produced by an ecosystem; i.e., this is gross primary production minus energy expenditures for autotrophic respiration (Odum, 1971, p. 43; Bazilevich, 1993, p. 8), or the amount of atmospheric carbon assimilated by the phytomass. Aggregated estimates of NPP are expressed in Tg (=10¹² g = million tons) of dry matter or carbon per year, and its average values per unit area (densities), in kg/m² per year. One-year intervals between aggregated NPP estimations are common, although this practice results in some unaccounted averaging: the life span of fine roots (≤ 2 mm) varies from weeks to years, depending on site conditions and plant species (Vogt and Bloomfield, 1991; Hendrick and Pregitzer, 1993), and there are data suggesting that the life cycle of trees in the boreal zone is longer (e.g., Kajamoto *et al.*, 1997).

The existing methods of NPP estimation on large territories include statistical approaches; climatic models; *gap* models; ecophysiological models of carbon flows, e.g., those using a chlorophyll index; remote sensing methods with the use of NDVI; models of production efficiency; and others. Each has its specific advantages and shortcomings, which are sometimes significant (Goetz, 1997; Mokronosov, 1999). As the purpose of this work was to evaluate the actual NPP of

Russian terrestrial ecosystems in general and over a certain period, the empiricism of statistical methods was an advantage rather than a shortcoming. In addition, any model approach needs verification, which is impossible without having a detailed empirical estimate of the NPP. Hence, a statistical method combined with a number of auxiliary “semi-empirical” models was used as the basis for our calculations.

As a function of time, the NPP of a certain plant formation or LULC class is a typical stochastic process and its parameters (in particular, variability) depend on specific seasonal features of the weather in a region and the pattern of natural disturbances associated with them. Therefore, any NPP estimate has limited significance if the corresponding period (year) is not indicated. On the other hand, both the available information and the methods applicable to the territories of countries as large as Russia significantly restrict the possibility of accurately identifying the time period. The results described in this paper are annual averages calculated over the period from 1988 to 1992.

MATERIALS AND METHODS

The basic methodological aspects of this work were outlined in the previous paper (Shvidenko *et al.*, 2000a). In particular, we adhered to the principles of the systems (holistic) approach and used geoinformation systems (GIS) as the main source of information

for calculations. NPP was estimated by the aggregated LULC classes, which included farmlands (with subdivision into arable lands, areas with perennial vegetation, and cultivated grasslands and pastures); forests; swamps and bogs; and natural grasslands and brushwoods. Estimations were based on the use of GIS technologies (primary polygons) and attributive databases (DBs) created at the International Institute for Applied Systems Analysis (IIASA) together with Russian collaborators. The DBs contained data on production by aggregated fractions (total green parts, aboveground woody parts, and underground parts) measured in more than 3000 test plots. For the LULC classes (excluding forests, arable lands, and cultivated pastures and grasslands), NPP was estimated by multiplying its average values in primary classification units of these classes (calculated from data obtained in test plots) by areas determined in the same way as in the study of phytomass stocks (Shvidenko *et al.*, 2000a). For arable lands and cultivated pastures and grasslands, it was assumed that the life cycle of plants is annual, i.e., the NPP in these LULC classes is equal to the phytomass stock. For forests, the total NPP and contributions of individual fractions to it were corrected using regression equations. Corrections were made for tree age and average growing stocks, which were determined for each ecoregion on the basis of data provided by the State Forest Inventory (SFI).

It is apparent that the NPP values determined in this way are approximate and concern ecosystems in a certain "quasi-stable" state, as both GIS data and climatic (weather) conditions are averaged over a certain period of time, statistical information is supplied with a delay, and the data on plant cover disturbances in the year or period of NPP assessment are incomplete. We attempted to improve the accuracy of the results by taking into account the most important natural and anthropogenic factors that have affected the ecosystems during the corresponding period. To this end, we developed a simplified expert system based on regional estimates of several parameters and processes.

First, we took into account the significant increase of production in northern ecosystems (in particular, those on permafrost) after various disturbances, especially fires. The mechanism of this increase has been studied fairly well (e.g., Fetcher *et al.*, 1984; Zimov *et al.*, 1999). Fires of medium intensity and frequency destroying the thick insulating layer of plant organic matter on the soil surface (1) increase the depth of the active soil layer, thus improving thermal and hydrologic conditions in habitats, and (2) increase the availability of nutrients to a significant extent, owing to fine roots (Chen and Harmon 1999). Similar changes occur under the effect of many other factors, such as the mechanical destruction of soils in the zones of intensive industrial development, but their extent and affected areas are smaller. The period of growth acceleration depends on the region, specific features of ecosystems, and many other endo- and exogenous factors; its aver-

age duration is 20–40 years. The process is difficult to describe quantitatively: the number of direct measurements is relatively small, and a large part of the zone is not under forest fire control. The burned-out areas in the unprotected zone can only be estimated by indirect methods, as remote sensing data on the entire Russian territory (or its greater part) are only available for 1987, 1992, and 1998 (Cahoon *et al.*, 1994, 1996; Street, 2000, personal communication). Nevertheless, we used these data for cross-checking the areas affected by fires in a continuous time series between 1961 and 1998. To construct this time series for the forest zone, we used regional SFI data (1961–1998) and the methods described by Shvidenko and Nilsson (2000). Burned-out areas in the tundra and subarctic regions were estimated by analogy with adjoining territories included in the SFI.

Second, we took into account the effect of wetland amelioration, which leads to a significant increase in the productivity of eutrophic and mesotrophic bogs (Valetov, 1992). The increase of NPP after various disturbances was determined on the basis of available publications, estimations of regional experts, and the results of our own measurements. In all cases, conservative estimates were chosen; if they were several, the estimate closest to the 25% quantile of their frequency distribution was used.

Third, we made an attempt to take into account the losses of the actual NPP in the areas affected by major types of disturbances in a given year, such as forest fires, large-scale tree felling, insect pest outbreaks, changes in the pattern of land use, and overgrazing. This concerned all the LULC classes except arable lands and cultivated pastures and grasslands. In forests, for example, the losses of production to animals and insects under normal conditions amount to 1–3% of the phytomass of auxiblasts and 2–6% of the current NPP of needles (Glazov, 1979). According to the results of expert evaluation, the accuracy of these corrections was not very high, but they changed the estimate of the total NPP by only 6.4% and, therefore, had no significant effect on the accuracy of final results.

Due to the amount of carbon accumulated over many years, forests deserve special attention in studies on estimating production, especially as concerns its important varieties such as *net ecosystem production* (NEP) and *net biome production* (NBP). For this reason, as well as for cross-checking the results obtained on the basis of GIS technologies, we estimated the gross and net increments in forests using the SFI data and an original modeling system. The methods and results of evaluating current increments in Russian forests were published previously (Shvidenko *et al.*, 1995, 1997). Below, these results will be used for comparison.

Table 1. Net primary production of terrestrial vegetation by land use/land cover classes and bioclimatic zones, Tg dry matter per year

Zone	Farmlands				Forests	Wetlands			Grasslands and brush-woods	Sum total
	Total	including				Total	including			
		arable lands	cultivated pastures	perennial vegetation			swamps	bogs		
Arctic and subarctic deserts	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.1	
Tundra	10.0	0.0	10.0	0.0	13.9	224.6	189.4	35.2	468.9	717.4
Forest–tundra, northern and sparse taiga	10.1	2.8	7.2	0.1	505.1	283.6	129.0	154.6	116.5	915.3
Middle taiga	122.7	59.9	62.2	0.6	2169.4	356.8	143.6	213.2	1188.1	3837.0
Southern taiga	395.6	315.1	75.5	5.0	690.5	173.4	11.6	161.8	266.7	1526.1
Temperate forests	301.8	239.2	54.9	7.7	196.1	13.0	5.0	8.0	55.3	566.2
Steppes	1131.9	781.0	346.4	4.5	96.9	17.0	12.3	4.7	505.5	1751.3
Semideserts and deserts	154.6	43.1	111.3	0.2	7.1	6.7	5.3	1.4	61.8	230.2
Total	2126.6	1441.0	667.5	18.1	3679.0	1075.1	496.2	578.9	2662.9	9543.7

Table 2. Net primary production of terrestrial vegetation by land use/land cover classes and bioclimatic zones, Tg C per year

Zone	Farmlands				Forests	Wetlands			Grasslands and brush-woods	Sum total
	Total	including				Total	including			
		arable lands	cultivated pastures	perennial vegetation			swamps	bogs		
Arctic and subarctic deserts	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.1	
Tundra	4.5	0.0	4.5	0.0	6.4	101.2	85.3	15.9	211.9	323.9
Forest–tundra, northern and sparse taiga	4.5	1.2	3.3	0.0	231.6	128.9	58.8	70.1	52.7	417.7
Middle taiga	55.3	26.9	28.0	0.3	1004.3	161.9	65.4	96.6	536.6	1758.1
Southern taiga	178.1	141.8	34.0	2.3	325.5	78.6	5.3	73.3	120.2	702.4
Temperate forests	135.9	107.6	24.7	3.5	91.8	5.9	2.3	3.6	24.9	258.5
Steppes	509.3	351.4	155.8	2.1	44.6	7.7	5.6	2.1	227.5	789.0
Semideserts and deserts	69.6	19.4	50.1	0.1	3.2	3.0	2.4	0.6	27.8	103.7
Total	957.2	648.5	300.4	8.3	1707.3	487.2	225.0	262.2	1201.7	4353.4

RESULTS AND DISCUSSION

Tables 1 and 2 show aggregated estimates of NPP by individual LULC classes, calculated using the GIS approach. According to them, the total NPP of Russian terrestrial ecosystems amounts to 9544 Tg of dry matter, or 4354 Tg C per year. For the quasi-stable state, NPP is estimated at 8969 Tg of dry matter, or 4090 Tg C per year; corrections for “actualization” add 575 Tg of dry matter, or 263 Tg C per year (6.4% of the quasi-stable estimate). A major part of production concentrates in forest ecosystems (39.2% by carbon); farmlands

account for 22.0%; grasslands and shrub communities, for 27.6%; and bogs and swamps, for 11.2%.

There are distinct zonal gradients of NPP both in the entire plant cover and within individual LULC classes (Table 3). In general, arable lands have the highest annual NPP values (498 g C/m²); then follow grasslands and brushwoods (278 g C/m²) and forests (224 g C/m²). Wetlands have the lowest NPP among the aggregated LULC classes (219 g C/m² per year), with marshlands being 5% more productive than bogs. From the zonal aspect, the largest NPP values for arable lands in the southern taiga zone and for forests in the steppe zone

Table 3. Density of net primary production of terrestrial vegetation by land use/land cover classes and bioclimatic zones, g C/m² per year

Zone	Farmlands				Forests	Wetlands			Grasslands and brush-woods	Sum total
	Total	including				Total	including			
		arable lands	cultivated pastures	perennial vegetation			swamps	bogs		
Arctic and subarctic deserts	0	0	0	0	0	0	0	8	8	
Tundra	245	0	245	0	168	162	160	178	106	121
Forest–tundra, northern and sparse taiga	288	404	260	0	164	199	208	192	207	179
Middle taiga	378	507	304	300	221	261	308	237	353	257
Southern taiga	504	587	325	329	257	260	326	257	616	332
Temperate forests	461	508	342	333	347	333	378	310	932	428
Steppes	456	468	430	350	482	1053	1091	966	854	532
Semideserts and deserts	402	449	386	400	254	916	929	867	431	409
Total	452	498	379	325	224	219	213	226	278	267

Table 4. Net primary production by major phytomass fractions and land use/land cover classes, Tg C per year

LULC class	Area, ×10 ⁶ ha	Net primary production, Tg C per year				Total NPP, Tg C per year ⁻¹
		green parts	woody parts	total aboveground	underground parts	
Arable lands	130.3	397.4	0.0	397.4	251.1	648.5
Cultivated pastures and grasslands	79.0	140.4	0.0	140.4	160.0	300.4
Areas under perennial vegetation	2.6	4.2	1.6	5.8	2.5	8.3
Total farmlands	211.9	542.0	1.6	543.6	413.6	957.2
Forests	763.5	836.2	451.1	1287.3	420.0	1707.3
Bogs	105.8	157.9	17.1	175.0	87.2	262.2
Swamps	116.2	113.4	16.6	131.0	94.0	225.0
Total wetlands	222.0	272.3	33.7	306.0	181.2	487.2
Grasslands and brushwoods	432.4	430.0	33.3	463.3	738.4	1201.7
Lands lacking vegetation	79.6					0.0
Sum total	1709.5	2080.5	519.7	2600.2	1753.2	4353.4

appear unusual, but this situation has a simple logical explanation. Forests of the tundra zone, which spread northward along the valleys of big rivers, are also slightly more productive than those of the forest–tundra zone (Pryazhnikov and Utkin, 1998). Small areas of wetlands in the steppe and semidesert zones (a total of about 1 million ha), mainly presented by grass bogs, have the highest NPP value among all the LULC classes. The average NPP of all Russian lands covered with vegetation (1629.8 million ha) is 267 g C/m² per year.

The distribution of NPP (carbon) by the LULC classes and aggregated fractions is shown in Table 4 and by the aggregated fractions and bioclimatic zones,

in Table 5. Green parts and aboveground wood accumulate 11.9% of this carbon, respectively. The proportion of underground NPP averages 40.3% but strongly varies depending on the LULC class. In individual classes, its proportions of the total NPP are as follows: 43.2% in farmlands, 24.6% in forests, 37.2% in wetlands (45.8% in bogs and 33.3% in swamps), and 61.2% in grasslands and shrub communities.

On the basis of GIS technologies, the NPP of aboveground wood in forests was estimated at 451.1 Tg C, or 902.2 g dry matter per year. To verify the result, this parameter was independently estimated from indices of the current increments (gross and net growth) of forest stands. The gross increment $dTV(A)$ is the amount of

Table 5. Distribution of net primary production (dry matter and carbon) by major phytomass fractions and bioclimatic zones

Zone	Net primary production, Tg dry matter per year					Net primary production, Tg C per year				
	Aboveground			Under-ground	Total	Aboveground			Under-ground	Total
	green parts	woody parts	total			green parts	woody parts	total		
Arctic and subarctic deserts	0.1	0.0	0.1	0.0	0.1	(0.1)	0	(0.1)	0	0.1
Tundra	326.0	17.6	343.6	373.8	717.4	146.7	8.8	155.5	168.4	323.9
Forest-tundra, northern and sparse taiga	424.0	109.2	533.2	382.1	915.3	190.8	54.6	245.4	172.3	417.7
Middle taiga	1854.9	590.0	2444.9	1392.1	3837.0	834.7	295.0	1129.7	628.4	1758.1
Southern taiga	774.4	243.4	1017.8	508.4	1526.2	348.5	121.7	470.2	232.4	702.4
Temperate forests	303.6	59.0	362.6	203.6	566.2	136.6	29.5	166.1	92.4	258.5
Steppes	832.7	18.4	851.1	900.2	1751.3	374.7	9.2	383.9	405.1	789.0
Semideserts and deserts	107.6	1.8	109.4	120.8	230.2	48.4	0.9	49.3	54.4	103.7
Sum total	4623.3	1039.4	5662.7	3881.0	9543.7	2080.5	519.7	2600.2	1753.2	4353.4

stem wood with bark (m^3) produced by a stand in the year A , and the net increment $dGS(A)$ is the difference between growing stock volumes in the end and in the beginning of this year; i.e., $dTV(A)$ and $dGS(A)$ reflect the contributions of stem wood to the net primary production and the net ecosystem production of a forest ecosystem, respectively. The expression $dM(A) = dTV(A) - dGS(A)$ is used for determining the current mortality (the loss of stem wood in the year A), which is usually divided into *natural*, *pathological*, and *mechanical*. In the 1990, the gross annual increment of all Russian forests was 1880 million m^3 , including 966.3 million m^3 of the net increment and 913.5 million m^3 of dead wood (52.2 and 47.8%, respectively) (Shvidenko *et al.*, 1997). Therefore, the annual average dGS , dM , and dTV values for the entire country were 1.27, 1.20, and 2.47 m^3/ha , respectively. These indices for individual regions differed significantly. For example, the respective values were 2.50, 2.25, and 4.75 m^3/ha in European Russia, compared to 0.92, 0.90, and 1.82 m^3/ha in Asian Russia. Thus, the average productivity of forests in Asian Russia was only 38% of that in European Russia. The relative mortality in forests was very high and reached 47.8% of the gross increment. This is explained by the prevalence of mature and over-mature forests in large areas, a high proportion of uneven-aged forests (up to 50–70% of the total area under mature and over-mature stands dominated by major forest-forming coniferous species of the taiga zone), and, especially, a high incidence of disturbances, mostly fires, in the Asian part of Russia.

In order to compare the gross increment and the NPP of aboveground woody parts in forests, it is necessary to calculate the gross increment growth of the crown wood, which should be added to that of the stem wood gross growth value. For this purpose, we used regression equations of the crown phytomass for major

forest-forming species (Shvidenko *et al.*, 2000b). At the average (by ecoregions) values of age, site index, and stocking, partial derivatives with respect to age showed the present rates of phytomass dynamics if the averages by ecoregion values of age, site index, and stocking are used, or, in different terms, the proportional part of the net ecosystem production accounted for generated by crown wood. Using such an approach, this proportion was estimated at 2.7% of the gross increment of the stem wood. The main factor accounting for this result is the advanced age of stands consisting of major forest-forming species: on the whole, the average age of conifers in Russia in the 1990s was 96 years; of hard-wooded deciduous trees, 116; and soft-wooded deciduous trees, 54 years. The average specific weight of wood in Russian forests was estimated at 495 kg/m^3 . Assuming that the $dM(A) : dGS$ ratio for stem wood could be applied to crown wood, we estimated the NPP of aboveground woody parts on the basis of the calculated current increment. The result was $1880 \times 0.495 \times 1.052 = 979.0$ Tg dry matter per year, compared to 902.2 Tg dry matter per year determined by the GIS method; as the difference from the latter value was relatively small (+8.5%), these two estimates could be regarded as consistent with one another.

According to our results, the NPP of Russian terrestrial ecosystems amounts to 7.9% of the global NPP, which was calculated by averaging 14 published estimates (55.2 Pg C per year), and its average density is about 66% of the global estimate, which is equal to 403 g C/ m^2 per year. There are only a few aggregated NPP estimates for all Russian terrestrial ecosystems, and we could not find any data on the NPP components in available publications. Voronin *et al.* (1995), using the chlorophyll index method, estimated the NPP of Russian terrestrial vegetation at 4409.7 Tg C per year.

The reported accuracy of the method is $\pm 15\text{--}25\%$ (Mokronosov, 1999). This and our results are nearly identical, differing by only 1.3%. However, although zonal NPP densities are similar, there are some systematic differences: our estimates are higher for grasslands, including arable lands (a probable effect of fertilizers?), and 10–15% lower for major taiga subzones, which is attributable to forest damage. In addition, there is a greater “hidden” difference, as Voronin *et al.* (1995) used a different distribution of lands by bioclimatic zones and LULC classes and considered the entire Russian territory, whereas we considered only the lands covered with vegetation. Nevertheless, their and our estimates are very close. The net primary production calculated for the restored plant cover on the basis of maps made by Bazilevich (1993) was 5204 Tg C per year, i.e., 19.5% higher than our estimate. The reasons for this were discussed in our previous paper (Shvidenko *et al.*, 2000a).

Published data on NPP in individual LULC classes and zones are more numerous. For Russian tundras, the annual NPP estimates of the last decade were 125 g C/m² (Karelin *et al.*, 1995), 109 g C/m² (Kolchugina and Vinson, 1993), and 0.075 g C/m²; for the forest–tundra zone, NPP was estimated at 125 g C/m² per year (Voronin *et al.*, 1995). Based on independent data, our estimate for the tundra zone (121 g C/m² per year) is nearly identical to that by Karelin *et al.* (1995). We calculated the average NPP for Russian boreal forests from average NPP densities in coniferous and deciduous forests of the circumpolar boreal zone, which were taken from ten publications available to us (for references, see Melilo *et al.*, 1993; Goldewijk *et al.*, 1994; Gower *et al.*, 1995; Schulze *et al.*, 1999) and weighed with respect to the areas under species of these groups. The result was 267 ± 89 g C/m² per year, i.e., approximately 12% higher than the estimate made in this study. The average NPP calculated from eight published estimates for forests of the temperate zone was significantly higher than our present estimate (by approximately 27%): 475 vs. 375 g C/m² per year. The differences appear relevant, taking into account that climatic conditions in huge forest areas in Siberia and the Russian Far East are more severe than in other territories of the circumpolar boreal zone, and estimates reported by different authors vary significantly (e.g., for boreal coniferous forests, from 123 to 419 g C/m² per year). In the recent paper by Gower *et al.* (2000), the reported NPP of Russian boreal forests is 614 g C/m² per year and the total average NPP for the entire circumpolar boreal zone is 424 g C/m² per year. The authors obviously overestimated both parameters, which is explained by the fact that their analysis was based on a limited amount of data on the most productive (southern Siberian) boreal forests. Therefore, these values should be regarded as average for the sample used by these authors, rather than average for all Russian boreal forests.

Using the approach briefly described in our previous paper (Shvidenko *et al.*, 2000a), the total NPP is calculated to a precision of about 7% (a priori confidential probability 0.9), with the uncertainty estimated by experts at about 11%. However, there are some doubts that could not be resolved on the basis of available information. One of the key problems in reliably estimating NPP concerns the analysis of production accounted for by fine roots (≤ 2 mm). We estimated the NPP of roots in general, without subdividing them into fine and coarse roots (it should be noted that the authors of some publications used in this work indicated that fine roots were taken into account in their studies, whereas a major part of the remaining papers simply provided references to the methods involving the measurement of fine roots). The result was 40.3% (of the total NPP) for all LULC classes and 24.6% for forests. The former value is in good correspondence with global estimates: assuming that fine roots have a one-year life cycle, Jackson *et al.* (1997) estimated their NPP at approximately 33% of the total production of the Earth's terrestrial vegetation. As to the NPP of fine roots in forests, this problem is open to discussion. There are two contradictory opinions, both supported by many publications [e.g., see discussions in Jackson *et al.* (1997) and Schulze *et al.* (1999)]: some authors claim that the NPP of fine roots in boreal forests is 38–40% of the total, whereas others estimate it at about 17–20%. It is known that this parameter in coniferous forests correlates with the annual average temperature and averages 60–90 g C/m² per year at 3°C and 100–130 g C/m² per year at 5°C (Raich and Nadelhoffer, 1989; Gower *et al.*, 1995). These values agree well with our estimates of underground NPP in forests by the bioclimatic zones. However, when we decided to test our calculations on the material collected by Bazilevich and randomly chose the data on 1094 plots in Russian forests growing in all bioclimatic zones, the average NPP of underground plant parts was estimated at only 16.1% of the total production. Taking into account the low accuracy of earlier methods for estimation the NPP of fine roots (Vogt *et al.*, 1986; Nadelhoffer and Raich, 1992) and the small number of measurements performed in the northern part of the boreal forest zone, we can assume that the available experimental data, at least in part, are characterized by systematic error and the value of this error is unknown. The solution of this problem is apparently impossible without systematic field measurements with the use of new methods and advanced measuring equipment, which have recently become available.

REFERENCES

- Bazilevich, N.I., *Biologicheskaya produktivnost' ekosistem Severnoi Evrazii* (Biological Productivity of Ecosystems in Northern Eurasia), Moscow: Nauka, 1993.
- Cahoon, D.R., Jr., Stocks, B.J., Levine, J.C., *et al.*, Satellite Analysis of the Severe 1987 Forest Fire in Northern China

- and Southeastern Siberia, *J. Geophys. Res.*, 1994, vol. 99, no. 18, pp. 627–638.
- Cahoon, D.R., Jr., Stocks, B.J., Levine, J.C., *et al.*, Monitoring the 1992 Forest Fire in the Boreal Ecosystem Using NOAA AVHRR Satellite Imagery, in *Biomass Burning and Climate Change*, vol. 2: *Biomass Burning in South America, Southeast Asia, and Temperate and Boreal Ecosystems, and the Oil Fires in Kuwait*, Levine, J.L., Ed., Cambridge, Mass.: MIT Press, 1996, pp. 795–802.
- Chen, H. and Harmon, M.E., Woody Root Decomposition, Carbon, and Nitrogen Dynamics in the Pacific Northwest, <http://www.fsl.orst.edu/~chenh/research/woodroot.htm>, 1999.
- Fetcher, N., Beaty, T.F., Mullinax, B., and Winkler, D.S., Changes in Arctic Tussock Tundra Thirteen Years After Fire, *Ecology*, 1984, vol. 65, pp. 1332–1333.
- Glazov, M.V., Structure and Specific Functional Features of the Biota in Southern Taiga Spruce Forests of Valdai, in *Organizatsiya ekosistem el'nikov yuzhnoi taigi* (Ecosystem Organization in Southern Taiga Spruce Forests), Moscow: Inst. Geogr. Akad. Nauk SSSR, 1979, pp. 10–39.
- Goetz, S.J., *Modeling Carbon Fluxes, Net Primary Production, and Light Utilization in Boreal Forest Stands*, Univ. of Maryland Press, 1997, p. 110.
- Goldewijk, K.K., van Minnen, J.G., Kreileman, G.J.J., Bloedfeld, M., and Leemans, R., Simulating the Carbon Flux between the Terrestrial Environment and the Atmosphere, *Water, Air, Soil Pollut.*, 1994, vol. 76, pp. 99–230.
- Gower, S.T., Isebrands, J.G., and Sheriff, D.W., Carbon Allocation and Accumulation in Conifers, in *Resource Physiology of Conifers: Acquisition, Allocation, and Utilization*, Smith, W.K. and Hinckley, T.M., Eds., Academic, 1995, pp. 217–254.
- Gower, S.T., Krankina, O., Olson, R.J., Apps, M., Linder, S., and Wang, C., Net Primary Production and Carbon Allocation Patterns of Boreal Forest Ecosystems, *Ecol. Appl.*, 2000.
- Hendrick, R.L. and Pregitzer, K.S., Patterns of Fine Roots Mortality in Two Sugar Maple Forests, *Nature*, 1993, vol. 361, pp. 59–61.
- Jackson, R.B., Mooney, H.A., and Schulze, E.-D., A Global Budget for Fine Roots Biomass, Surface Area, and Nutrient Contents, *Proc. Natl. Acad. Sci. USA*, 1997, vol. 94, pp. 7362–7366.
- Kajimoto, T., Matsuura, Y., Sofronov, M.A., *et al.*, Above- and Below-Ground Biomass and Annual Production Rates of a *Larix gmelinii* Stand near Tura in Central Siberia, *Proc. Fifth Symposium on the Joint Siberian Permafrost Studies between Japan and Russia in 1996*, Inoue, G. and Takekawa, A., Eds., Tsukuba: NIES, 1997, pp. 119–129.
- Karelin, D.V., Zamolodchikov, D.G., and Gil'manov, T.G., Carbon Stocks and Production in the Phytomass of Russian Tundra and Forest–Tundra Ecosystems, *Lesovedenie*, 1995, no. 5, pp. 29–36.
- Kolchugina, T.P. and Vinson, T.S., Carbon Sources and Sinks in Forest Biomes of the Former Soviet Union, *Global Biogeochem. Cycles*, 1993, no. 7(2), pp. 291–304.
- 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.
- Mokronosov, A.T., Global Photosynthesis and Plant Biodiversity, *Krugovorot ugleroda na territorii Rossii* (Carbon Cycle on the Russian Territory), Moscow: Ross. Akad. Nauk, 1999, pp. 19–62.
- Nadelhoffer, K.J. and Raich, J.W., Fine Root Production Estimates and Belowground Carbon Allocation in Forest Ecosystems, *Ecology*, 1992, vol. 73, no. 4, pp. 1139–1147.
- Odum, E.P., *Fundamentals of Ecology*, Philadelphia: Saunders, 1971, 3rd ed.
- Pryazhnikov, A.A. and Utkin, A.I., Larch Forests and Open Woodlands of Russian Subarctic, in *Ekologiya taezhnykh lesov* (The Ecology of Taiga Forests), Syktyvkar, 1998, pp. 94–95.
- Raich, J.W. and Nadelhoffer, K.J., Belowground Carbon Allocation in Forest Ecosystems: Global Trends, *Ecology*, 1989, vol. 70, pp. 1346–1354.
- Schulze, E.D., Lloyd, J., Kelliher, F.M., *et al.*, Productivity of Forests in the Eurosiberian Boreal Region and Their Potential to Act as a Carbon Sink: A Synthesis, *Global Change Biol.*, 1999, no. 3, pp. 703–722.
- Shvidenko, A.Z. and Nilsson, S., Fire and Carbon Budget of Russian Forests, in *Fire, Climate Change, and Carbon Cycling in the Boreal Forest*, Kasischke, E. and Stocks, B., Eds., Springer, 2000, pp. 289–311.
- Shvidenko, A., Venevsky, S., Raile, G., and Nilsson, S., A System for Evaluation of Growth and Mortality in Russian Forests, *Water, Air, Soil Pollut.*, 1995, vol. 88, pp. 333–350.
- Shvidenko, A., Venevsky, S., and Nilsson, S., Generalized Estimation of Increment and Mortality in Russian Forests, *Sustainable Development of Boreal Forests, Proceedings of the 7th Annual Conference of the IBFRA, August 19–23, 1996, St. Petersburg*, Federal Forest Service of Russia, Moscow, 1997, pp. 184–191.
- Shvidenko, A.Z., Nilsson, S., Stolbovoi, V.S., *et al.*, Aggregated Estimation of Basic Parameters of Biological Production and Carbon Budget of Russian Terrestrial Ecosystems: 1. Stocks of Plant Organic Mass, *Ekologiya*, 2000a, vol. 31, no. 6, pp. 403–410.
- Shvidenko, A., Nilsson, S., Shepashenko, D., and Lakida, P., Models for Aggregated Estimations of Forest Ecosystems Phytomass of Northern Eurasia, *IR, International Institute for Applied Systems Analysis*, Laxenburg, Austria, 2000b.
- Valetov, V.V., Phytomass and Primary Production of Woodless and Forest Bogs: An Example of Northern Belarus, *Doctoral (Biol.) Dissertation*, Moscow: Inst. of Forestry, Russian Academy of Sciences, 1992.
- Vogt, K.A. and Bloomfield, J., Tree Root Turnover and Senescence, in *Plant Roots: The Hidden Half*, Waisel, A.E.Y. and Kafkafi, U., Eds., New York: Marcel Dekker, 1991, pp. 281–306.
- Vogt, K.A., Grier, C.C., Gower, S.T., *et al.*, Overestimation of Net Root Production: A Real or Imaginary Problem?, *Ecology*, 1986, vol. 67, no. 2, pp. 577–579.
- Voronin, P.Yu., Efimtsev, E.I., Vasil'ev, A.A., Vatkovskii, O.S., and Mokronosov, A.T., Projective Chlorophyll Content and Plant Biodiversity in the Main Botanical–Geographic Zones of Russia, *Fiziol. Rast.*, 1995, vol. 42, pp. 295–302.
- Zimov, S.A., Davidov, S.P., Zimova, G.M., *et al.*, Contribution of Disturbance to Increasing Seasonal Amplitude of Atmospheric CO₂, *Science*, 1999, vol. 284, pp. 1973–1976.