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Production and Destruction of Plant Organic Matter in Bog Ecosystems in the South of Western Siberia

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ABSTRACT: There are still many gaps in studies of the carbon cycle in northern ecosystems. It is challenging also in the context of climate change. This new study focuses on providing the state of the art data on the dynamics of plant organic matter, namely, the live plant biomass (phytomass), the dead biomass (mortmass), the Net Primary Production (NPP), as well as the rate of decomposition of plant organic matter of the major plant species, contributed to peat deposits. The study was conducted via direct in–situ measurements of different fractions of plant organic matter at a few test sites of oligotrophic pine–dwarf shrub–*Sphagnum* bogs at a wide geographic gradient (from the middle taiga to the forest-steppe regions in Western Siberia) based on an original methodology of measurements developed by the authors. In general, the five groups of plant species were distinguished in terms of productivity and decomposition rates. The study revealed a strong correlation between the net primary production (NPP) and the rate of decomposition of plant organic matter in pristine northern peatlands: an increase in productivity (NPPs) was basically leading to an increase in rates of decomposition in all plant materials collected in bog ecosystems. The study contributes to a global understanding of patterns and main drivers related to basic set of carbon cycle components in the northern wetland (peatland) ecosystems, their diversity and their spatial distribution.

Keywords: Plant biomass; Net Primary Production (NPP); Destruction of plant organic matter; Carbon sequestration; Wetlands/peatlands; Western Siberia

1. Introduction

Despite covering only 3% of the earth's land surface, the northern peatlands—defined as the area north of 50° N—store approximately 15–30% (200–455 Pg (=10^{15} g)C) of the total terrestrial pool of soil carbon in undecomposed peat [1–3]. Western Siberia is located in the central part of the Eurasian continent, where its area accounts for 2.4 million km^2. The area is a point of interest for several carbon cycle studies due to the wide spread of peat accumulation processes. Still, it remains a white spot, as remote and difficult to access region. The peatlands (or peat-accumulating wetlands) occupy about 34% (in some areas up to 75–80%) of the region, and they contain 36% of the total pool of soil carbon in Russia [4–9]. The peatlands in Western Siberia are known to play a key role in the formation of the regional climate, regulation of river flows, and carbon fluxes to the atmosphere, and all those, in turn, significantly contribute to the global carbon cycle.

The term "oligotrophic (pine–dwarf shrub–*Sphagnum*) bog, or ryam" refers to peatland that exists in specific conditions of water– and mineral supply; its "domed" shape of the land surface is formed at a certain stage of peat bog developments [4,10–12]. The ryam is the most common type of peatland in the boreal region of Western Siberia. They occupy the lower landscape elements and topographical depressions, and they make boundary areas of large wetland

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massifs. In the forest–steppe region of Western Siberia, the bogs currently exist at the southern climatic limit of distribution. Still, the ryam yet remains one of the most common regional types.

The carbon balance of natural peatlands is determined by the ratio of carbon uptake by plants (via the stock of live biomass and net primary production, NPP) and the decomposition of different fractions and species formed by the plant community [13]. The studies of production and destruction processes along the climatic (latitudinal) gradient are an important measure of environmental change that manifests in notable changes in the structure of plant communities and the composition of plant species.

In a number of countries such as England, the USA, Canada and Finland, the production and destruction processes in natural peatlands have been actively studied since the middle of the 20th century [14–21]. In the territory of the Former Soviet Union (FSU), similar studies were conducted in Belarus, Karelia, Western Siberia, and the Far East [22–29].

A few studies revealed that the rate of decomposition of plant organic matter depends on the type of plant communities and the composition of different fractions in plant organic materials. Among them, the leaves of vascular plants and grasses decompose faster, and the sedges decompose at somehow slower rates. Still, the slowest rate of decomposition was observed in *Sphagnum* mosses [23,29–31]. Moreover, the decomposition was found at higher rates in the rich nutrients ecosystems; the high net primary production (NPP) and high input of plant matter into the ecosystem also suggest higher decomposition rates [32]. A number of earlier publications [26,28,32–38] made it possible to reveal the features of the biological carbon cycle at the regional scale and to evaluate its basic characteristics. The studies concluded that peatlands represent the natural carbon reservoir as ecosystems with a positive carbon balance. Indeed, peat deposits accumulated during the Holocene presented clear evidence of the effectiveness of this process. However, some studies suggested reliable data to consider *Sphagnum* bogs as a source of carbon dioxide to the atmosphere at the current state of their development [39]. Overall, it can be assumed that raised peat-accumulating bogs represent carbon sinks in their current state, but even minor changes in climatic conditions can potentially change their carbon balance in the direction of the carbon sources [40–42].

The buildup of carbon dioxide (CO_2) in the atmosphere and the resulting global warming have the potential to affect both production and destruction processes in natural ecosystems, which in turn has the potential to affect carbon storage of wetland ecosystems, particularly in the northern high latitudes [43]. This study intended to analyse the features of production and destruction processes on contrasting examples of the pine–dwarf shrub–*Sphagnum* bogs along a wide latitudinal gradient: in the forest–steppe and in the south– and middle boreal (taiga) regions in Western Siberia. Hereby, we present a new assessment of the values of live plant biomass (phytomass), dead plant biomass (mortmass), and net primary production (NPP), as well as the decomposition of plant organic matter and its deposition to peat sediments.

2. Materials and Methods

The wetland/peatland ecosystems have been developed in optimal climatic conditions in the boreal region of Western Siberia since the early Holocene and till present [40,44,45]. However, a certain deficiency of moisture and high temperatures represent, the main climate constraints at the southern climatic limit of the boreal region (co-called, the forest-steppe region). The main features of climates at the study sites are presented in Table 1. In the middle boreal (taiga) region, the existence of peatlands is supported by the high amount of precipitation and fairly cool temperatures, which lead to the highest area coverage. In the south, the peatlands increase their productivity and retain a large area of distribution. The largest wetland/peatland system, the Great Vasyugan mire, is located in the southern taiga region. In the forest–steppe, oligotrophic bogs (ryams) occupy a very limited area and, due to a lack of moisture, its productivity remains low [46,47].

The average annual temperature is close to zero only in the south taiga and in the forest-steppe; in the region of the middle taiga, it accounts for –1.3 °C (Table 1). The maximum precipitation occurs in the summer and early autumn time periods, which corresponds well to the growing season.

Table 1. Climatic conditions of different geographic regions in the south of Western Siberia: the mean annual precipitation (mm) and mean annual temperature (t °C).

Region	Annual Precipitation, mm	Annual Mean Temperature, t °C	Height above Sea Level (HMSL), m
middle boreal (taiga)	470	−1.3	50–100
south boreal (taiga)	408	−0.4	50–150
forest steppe	347	−0.1	100–150

The study was carried out at three test sites of oligotrophic (poor of nutrients) peat bog ecosystems corresponding to three geographic regions presented in Table 1. These bog ecosystems do not differ in terms of landscape appearance also in terms of composition of the dominant species in the shrub-grasses and moss layers; all represent the forested pine (*Pinus sylvestris* L.) dwarf shrub–*Sphagnum* (ryam type) raised bogs. The forested peatlands account for 58% of the entire boreal region. In contrast, they account for only 9% of the forest–steppe of Western Siberia, but they still represent a typical regional peatland type [32,48,49].

The forest-steppe test site is located in the topographical depression in the Ubinsky district of the Novosibirsk region near the settlement of Nikolaevka (55°09′09.9″ N; 79°02′43.5″ E), Figure 1. Here, the peatlands developed under variable moisture conditions that constrain their progressive growth [50]. Being on the range of their geographical distribution, they do not form large peatland massifs but exist in the landscape as separate spots and therefore are very vulnerable to changes in environmental conditions. The woody layer is formed by pine trees (*Pinus sylvestris*) 10–12 m high and crowns in the upper third of the trunk. The undergrowth contains some small pine and birch (*Betula pubescens* Ehrh) trunks, 0.5–3 m high. The shrub layer of 50–70 cm high is presented by a number of species: *Ledum palustre* L.—40%, *Chamaedaphne calyculata* (L.) Moench—20%, *Andromeda polifolia* L.—5%, *Vaccinium vitis-idaea* L.—10%, *Oxycoccus palustris* Pers.—3%, *Oxycoccus microcarpus* Turcz. ex Rupr.—2% of land projective cover. Herbaceous plants presented by *Rubus chamaemorus* L. and *Eriophorum vaginatum* L. The mosses have a projective cover of close to 100% and comprises of *Sphagnum fuscum* (Schimp.) H. Klinggr.—60%, *S. capillifolium* (Ehrh.) Hedw.—30%, *S. angustifolium* (C. Jensen ex Russow) C. Jensen—9%, *Polytrichum strictum* (Brid.) Mitt occurs—1%. The depth of peat deposits ranges from 2 to 4 m as measured at different locations.

The south taiga test site belongs to so–called "Bakchar" peatlands, located within a large Vasyugan wetland system (56°51′17.9″ N; 82°50′59.9″ E), Figure 1 [51,52]. This area is included in the zone of domed oligotrophic wetlands [53]. In this region, the peat-accumulating wetlands occur at 45 to 80% of the land surface [54]. The land cover in this bog (or ryam) ecosystems is represented by pine–dwarf shrub–*Sphagnum* plant communities, with the dominance of pine *Pinus sylvestris*-in the tree layer, the height of 2–4 m. The shrubs and grasses are presented by *Chamaedaphne calyculata* and *Ledum palustre* on 50–80 cm high tussocks, and *Eriophorum vaginatum*, *Andromeda polifolia*, *Rubus chamaemorus* and *Oxycoccus palustris* distributed sporadically in inter–tussock depressions. The projective cover of shrubs is 40–50%. The tussocks are well developed in micro–landscape and contribute up to 70% of land cover. The moss layer is dominated by *Sphagnum fuscum*—60% and *S. divinum* Flatberg & Hassel—20% of projective cover on the tussocks; and *S. angustfolium* in inter–tussock depressions, which contribute about 50% of projective cover. The depth of peat deposits does not exceed 2 m.

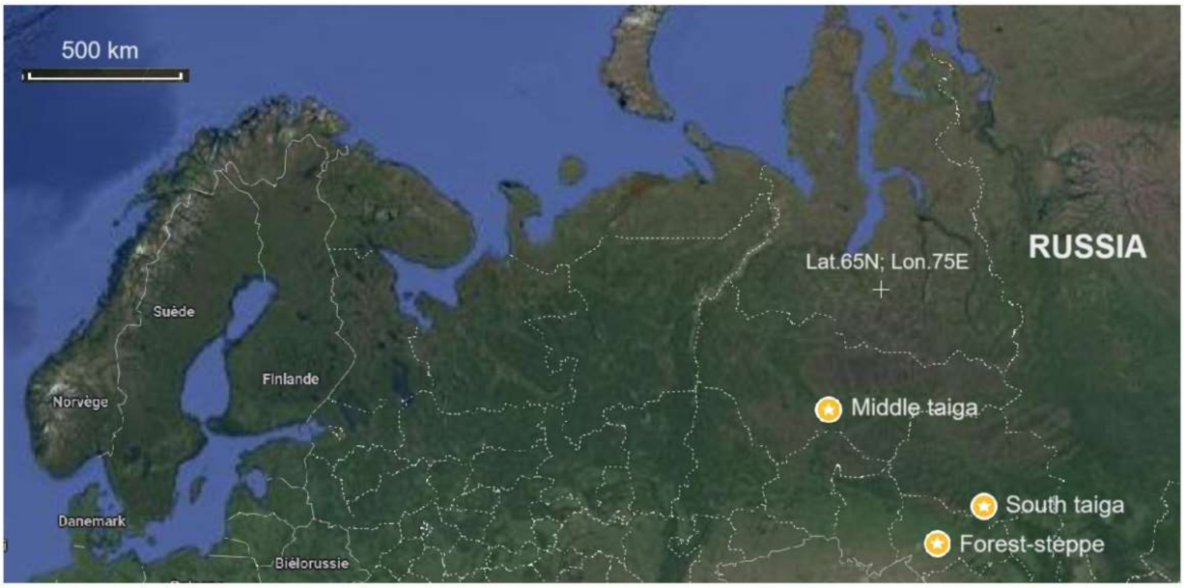

Figure 1. Location of study sites (at the Google maps view, available at https://www.google.com/maps/, accessed 16 October 2023), where the "forest–steppe" corresponds to study site centered at 55°09′09.9″ N; 79°02′43.5″ E; the "south taiga"—study site centered at 56°51′17.9″N; 82°50′59.9″ E, the "middle taiga"—study site centered at 60°58′07.8″ N; 70°10′50″ E; the last two study sites located in a boreal region of Western Siberia.

The middle taiga test site is located in the interfluve of the Ob and Irtysh rivers, 65 km east of the city of Khanty–Mansiysk (60°58′07.8″ N; 70°10′50.0″ E), Figure 1. The feature of the area is a high diversity of wetland ecosystems. The plant community of studied pine–dwarf shrub–*Sphagnum* bog in this region is very similar to the forest–steppe and the south taiga test sites in terms of the main species composition. The woody layer is represented by pine trees; among the shrubs, on the tussocks, there was found a high abundance of *Ledum palustre*, *Oxycoccus microcarpus* and *Chamaedaphne calyculata*; *Andromeda polifolia* in the inter–tussock depressions. In general, projective cover of shrubs accounted for 50 to 65%. The moss layer is formed by *Sphagnum fuscum* with a projective cover of about 85%. The depth of peat deposits ranges from 1.5 to 2.0 m.

To estimate biological productivity, the sampling was carried out based on conventional methods of in–situ measurements that subscribe to collecting the samples of plant materials in a range of most typical points at the test site, taking into account the features of microtopography. At selected test sites, the samples of plant organic matter were taken at each 10–cm depth layer by layer to a depth of 30 cm. The vascular plants, including the shrubs and herbs/grasses, were cut above the land surface from 40 × 40 cm square frames in the amount of 7–10 samples at the end of the growing season. The mosses and the roots systems of grasses and shrubs were removed in a square sampling instrument of 1 dm^3 from the surface of the moss heads. In the laboratory, the samples were divided into a few fractions: photosynthetic (green) parts of grasses, shrubs, and mosses (also divided by tips and stems), all annual and perennial shoots of shrubs, live and dead below-ground organs of grasses and shrubs, and buried stems. The fractions of plant organic matter were dried to an air–dry state at a temperature of 60 °C and then weighed.

The number of trunks, height, diameter and age were determined for the trees. The model trees were selected with 2–5 mm trunk diameter increments. Further, the model trees were divided into fractions to separate different vegetative organs and to determine their age. The stock of different phytomass fractions (needles and shoots of the current, last and year before last, perennial shoots, trunks) was calculated using the regression method as a function of the diameter of the trunk at the level of the moss cover [46].

Net primary production (NPP) consists of the above-ground production of trees, grasses, shrubs and mosses (ANP) and the production of below-ground organs of plants (BNP). Above-ground production of grasses represents all fractions of photosynthetic (green) phytomass. The below–ground production of grasses and shrubs was determined by the current year's growth of roots, rhizomes and tillering nodes. Above–ground production of shrubs refers to the growth of branches of the current year with leaves growing on them [55]. The production of *Sphagnum* mosses was determined using the "individual tags" method developed by N.P. Kosykh in 1999 [56]. Below–ground production of grasses and shrubs was determined by the growth of roots, rhizomes and tillering nodes of the current year [57].

In bog ecosystems, in–situ, experiments were made to determine the rate of decomposition of peat-forming plants by bury of plant organic materials in peat deposits [58]. For this purpose, in the fall season, the typical wetland plants

(*Sphagnum angustifolium*, *S. divinum*, *S. fuscum*, *Andromeda polifolia*, *Ledum palustre*, *Betula nana* L., *Vaccinium vitis-idaea*, *Chamaedaphne calyculata*, *Oxycoccus palustris*, *Pinus sylvestris*, *Rubus chamaemorus*, *Eriophorum vaginatum*) were collected from all test sites. The dried samples weighing 1 g were packed in nylon bags and placed in a peat deposit to a depth of 5–15–25 cm below the land surface. After 12 months–long exposition, the loss in the weight of plant organic matter was determined for each sample by the gravimetric method [23]. Destruction of organic materials was studied by analysing of the rate of decomposition, and the loss of weight was calculated as a percentage of the original weight. The total losses of plant organic matter during the exposition of dead phytomass were presented for all fractions and for different wetland ecosystems, considering the coefficients of decomposition derived from experiments. It was assumed that the peatlands are in dynamic equilibrium and the created annual production is equal to the amount of phytomass that dies in certain ecosystems on an annual basis [38].

3. Production and Destruction of Plant Organic Matter

3.1. The Stock of Biomass in Bog Ecosystems

The stock of biomass, where the total biomass is composed of two fractions: (i) live biomass (or phytomass) and (ii) dead biomass (or mortmass) presented in Table 2 and Figure 2. The total biomass accounted for the lowest value of 8917 ± 832 found in the southern boreal region. In contrast, rather similar values of 12,779 ± 2528 and 12,274 ± 650 were found in the forest-steppe and in the middle taiga regions, respectively. Overall, the data display no trend in change of biomass values along geographical gradient. Still, the total biomass was to be about 40% less in the southern taiga regionfound in other regions. The same trend was found in the geographical distribution of dead biomass (mortmass), with the lowest values of 4741 ± 183 in the southern taiga region and with very similar values of almost two folds higher in other regions.

Table 2. The stock of live (phytomass) and dead (mortmass) fractions of biomass in bog ecosystems (g/m^2) and its standard deviation (±SD). The figures presented in dry organic matter.

Fraction of Biomass	Middle Taiga	Southern Taiga	Forest Steppe
live biomass (phytomass)	3508 ± 242	4176 ± 156	3957 ± 191
dead biomass (mortmass)	8766 ± 832	4741 ± 183	8822 ± 2348
total biomass	12,274 ± 650	8917 ± 47	12,779 ± 2528

Overall, the dead fraction of biomass (mortmass) predominates in biomass structure in all studied ecosystems. It contributes 53% of the total biomass in the bog ecosystems of the southern taiga region and about 70% of the total biomass in other regions. Mortmass predominates live biomass even in the active upper layer of peat deposits where the main biological processes occur (the data are not presented). It is formed by decomposing residues of mosses and vascular plants buried in peat deposits at different times.

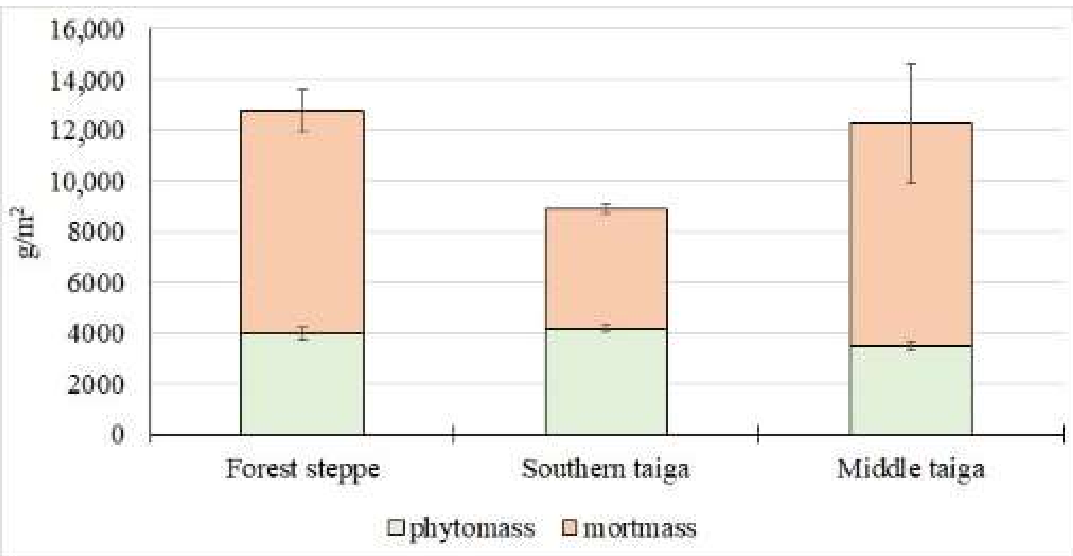

Figure 2. Regional distribution of live (phytomass) and dead (mortmass) fractions of biomass in bog ecosystems (g/m^2). The error bars refer to standard deviation (SD).

The fraction of dead biomass in the active layer reflects the type of biological cycle, where climatic conditions are the main drivers of organic matter turnover and carbon accumulation. Along them are the type of water and nutrient supply and water table in bog ecosystems. The above-ground mortmass, by definition consists of so–called, "vetosh" (which is slightly decomposed plant organic matter that remains the structure of original plant materials and is still connected with plants). Its lowest values were found in oligotrophic hollows, where the litter mineralizes quickly. The higher values of above–ground mortmass were found on elevated topographical elements, such as ridges in ridge–hollow mires and bog ecosystems; it also includes the leaves of evergreen shrubs, which slowly decompose, and can be accumulated at the land surface over several seasons.

The study revealed rather minor differences in the values of live biomass (phytomass) across all ecosystems. The lowest values (3508 ± 242) were found in bog ecosystems of the middle taiga, and the highest values (4176 ± 156) were found in bog ecosystems of the southern taiga. Hereby, we confirm no geographical trend can be derived from our studies of live biomass stock in a range of studied ecosystems.

About half (40–45%) of the live biomass was contributed by pine trees (*Pinus sylvestris*), of which the main contribution was made by trunks and branches—30%; the tree roots accounted for about 10%, and the needles accounted for 4–6%. The number of pine trees was 3.4 ± 1.2 thousand per ha^{-1} in the forest-steppe, 12.5 ± 2.6 thousand trunks per ha^{-1} in the middle taiga, and the highest values of 20.3 ± 6.6 thousand trunks ha^{-1} in the southern taiga. The average height of pine trees was found to be 173 ± 19 cm at bog sites in the forest–steppe region, 106 ± 3 cm in the southern taiga, and 103 ± 3 cm in the forest steppe; then it tends to decrease from south to north along a geographical gradient in our study. The average diameter at the surface of the moss cover ranged from 30 ± 4 mm in the forest-steppe, to 25 ± 1 in the southern taiga, and to 20 ± 1 mm in the middle taiga regions. The age of forest stands at study sites was usually limited to 80–100 years, with the largest contribution from young trees (up to 11 years old) in the forest–steppe, and up to 40 years old in the taiga regions.

The green (photosynthetic) phytomass of the trees, i.e., tree needles, in the forest–steppe region was found at 120 ± 25 g/m^2. In contrast, it accounted for 129 ± 15 g/m^2 in the middle taiga and 270 ± 55 g/m^2 in the southern taiga (Table 3, Figure 3). Above–ground organs of trees, i.e., trunks and branches, contributed 344 ± 78 g/m^2 (34%) of live biomass in the forest–steppe, and 1300 ± 268 (71%) and 1123 ± 225 g/m^2 (71%) in the southern and in the middle taiga, respectively.

Table 3. Live biomass (phytomass) of pine trees (*Pinus sylvestris*), g/m^2 and its standard deviation (±SD). The figures presented in dry organic matter.

Fractions of Live Biomass	Middle Taiga	Southern Taiga	Forest Steppe
trunks and branches	1123 ± 225	1300 ± 268	344 ± 78
tree needles	129 ± 15	270 ± 55	120 ± 25
tree roots	333 ± 107	250 ± 73	547 ± 65
Total of pine trees	1585 ± 301	1820 ± 364	1011 ± 203

The total stock of above–ground biomass in tree layer was estimated at 464 ± 92 g/m^2 in the forest–steppe, 1570 ± 248 g/m^2 in the southern taiga and 1252 ± 240 g/m^2 in the middle taiga regions, which corresponded to the contribution of pine trees to the total above–ground biomass of bog ecosystems of 31% in the forest–steppe, 59% in the southern taiga and 46% in the middle taiga regions.

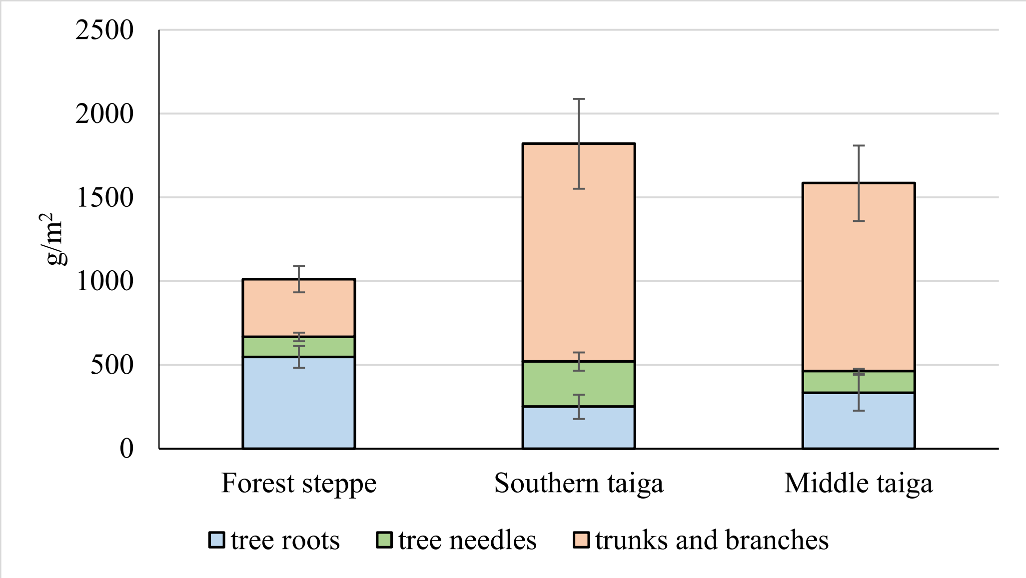

Figure 3. Live biomass (phytomass) of pine trees (*Pinus sylvestris*), g/m^2. The error bars refer to standard deviation (SD).

The data of live biomass other than the tree layer (i.e., mosses, grasses, and shrubs) are presented in Table 4. Overall, the major contribution of about 40% was made by shrubs, of which the roots contributed about 30%, the stems—5%, and the leaves did not exceed 3%. In addition, about 10% of biomass contributed by mosses. The contribution of grasses was very minor (it does not exceed 1%).

Table 4. Non–wooden live biomass (phytomass)—moss, grasses, and shrubs, in g/m^2 and its standard deviation (±SD). The figures presented in dry organic matter.

Plant Species	Fractions	Middle Taiga	Southern Taiga	Forest Steppe
Andromeda polifolia	leaves	8 ± 0.6	3 ± 1	15 ± 2
	stems	58 ± 3	1 ± 0.1	33 ± 3
Chamaedaphne calyculata	leaves	26 ± 2.7	118 ± 12	25 ± 3
	stems	232 ± 16	160 ± 11	81 ± 7
Ledum palustre	leaves	63 ± 10	10 ± 1	72 ± 14
	stems	511 ± 62	11 ± 2	113 ± 13
Oxycoccus palustris	leaves	4 ± 1	4 ± 1	8 ± 3
	stems	91 ± 12	2 ± 1	0
Vaccinium vitis-idaea	leaves	1 ± 1	1 ± 1	7 ± 2
	stems	1 ± 1	4 ± 1	6 ± 2
Total of roots		333 ± 54	1235 ± 110	1840 ± 228
Total of shrubs		1328 ± 302	1549 ± 156	2200 ± 241
Rubus chamaemorus	leaves	11 ± 3	4 ± 1	8 ± 3
	roots	133 ± 17	36 ± 22	86 ± 16
Total of grasses		144 ± 17	40 ± 21	94 ± 19
Sphagnum fuscum		451 ± 87	767 ± 58	652 ± 42
Total biomass (phytomass)		1923 ± 302	2356 ± 184	2946 ± 191

Despite the same type of bog ecosystems and similar structure of plant communities at all studied sites, some important differences in biomass structure were identified (see Table 4). More severe climatic conditions in the boreal (taiga) regions make certain constraints to live biomass reserves and, generally, the productivity of bog ecosystems. The live biomass of the grass–shrub–moss layer was found in the range of 1923 ± 302 and 2356 ± 184 g/m^2 across taiga ecosystems, whereas it accounted for 2946 ± 191 g/m^2 and in the forest–steppe, so the values increased by 23% on the transition from middle taiga to southern taiga regions. It was further increased by 30% on the transition to the forest steppe region. The live biomass of mosses (*Sphagnum fuscum*) varied from 451 ± 87 to 767 ± 58 g/m^2. The highest values of live biomass were found in bog ecosystems of southern taiga, which have a high density of peat deposits and the longest growing season for wetland plants among all studied ecosystems. In the driest areas of the bogs, the stems of shrubs predominated in the above-ground fraction of live biomass.

When we consider the tree (wooden) layer, it contributes an additional 45% to the live biomass value in the boreal (taiga) region and adds 26% to the live biomass value in the forest-steppe region. Thus, the total live biomass, including the wooden layer, accounted for 3508 ± 242 g/m^2 in the middle taiga. The maximum value of 4176 ± 156 g/m^2 is achieved in the southern taiga, then it decreased again to 3957 ± 191 g/m^2 in the forest-steppe region (all numbers correspond to the total live biomass values in Table 2).

3.2. The Net Primary Production (NPP) in Bog Ecosystems

The Net Primary Production (NPPs) of different fractions studied at three study sites are shown in Table 5 and Figure 4. There was no geographical gradient revealed in a spatial distribution of productivity of bog ecosystems that could be driven by different climatic conditions. The most productive ecosystems were found in the bogs in the forest steppe region. Across the fractions of mosses, grasses, shrubs and trees in these ecosystems, its' ratio could be described as follows: 8:1:12:4.

Table 5. Net Primary Production (NPP) in pine–dwarf shrub–*Sphagnum* bogs, in g/m^2/yr m^2 and its standard deviation (±SD). The figures presented in dry organic matter.

Plant Species	Fractions	Middle Taiga	Southern Taiga	Forest Steppe
Pinus sylvestris	needles	27 ± 3	61 ± 11	37 ± 5
	branches	9 ± 1	10 ± 3	10 ± 2
	roots	43 ± 5	61 ± 11	69 ± 15
Above-ground NPP of trees		36 ± 4	71 ± 8	47 ± 6
Total NPP of pine trees		79 ± 8	132 ± 14	116 ± 22
Andromeda polifolia	leaves	4 ± 0.9	2 ± 0.3	8 ± 4
	stems	2 ± 0.7	1 ± 0.1	3 ± 2
Chamaedaphne calyculata	leaves	18 ± 3	71 ± 6	22 ± 4
	stems	6 ± 0.5	17 ± 2	10 ± 1
Ledum palustre	leaves	31 ± 3	6 ± 2	50 ± 11
	stems	7 ± 1.5	2 ± 0.8	20 ± 5
Oxycoccus palustris	leaves	1 ± 1	2 ± 1	0
	stems	0	1 ± 0.4	0
Vaccinium vitis-idaea	leaves	1 ± 1	1 ± 0.1	7 ± 5
	stems	0	0	2 ± 1
Above-ground NPP of shrubs		70 ± 26	102 ± 10.5	122 ± 9
NPP, roots of shrubs		266 ± 35	190 ± 13	383 ± 183
Rubus chamaemorus	leaves	11 ± 3	1 ± 0.3	0
	roots	67 ± 23	4 ± 1.6	0
Moss *(Sphagnum fuscum)*		232 ± 4	250 ± 30	257 ± 14
Total NPP of non-wooden component		646 ± 42	547 ± 19	762 ± 182
Total NPP		725 ± 123	680 ± 19	878 ± 141

Overall, the pine trees made a rather minor contribution to NPPs, so the majority of NPPs were created by non-–wooden components. Above–ground primary production of the tree layer was calculated as the sum of the stocks of needles of the current year and shoots of trunks of the current year and accounted for 47 ± 6 g/m^2 per year in the forest–steppe; for 71 ± 8 g/m^2 per year in the southern taiga; and it drops to 36 ± 4 g/m^2 per year in the middle taiga. The contribution of pine trees (both the above– and below–ground components) to the total net primary production (NPP) of bog ecosystems accounted for 11%, 19%, and 13% in the middle taiga, the southern taiga, and the forest-steppe regions, respectively. The NPPs of pine trees stayed in the range of 79 ± 8 g/m^2/yr in the middle taiga and 132 ± 14 g/m^2/yr in the southern taiga, whereas it was 116 ± 22 found in the forest-steppe region.

When we exclude the contribution of pine trees' NPPs, then higher production was found in the bog ecosystems of forest–steppe region (Table 5). Some longer growing seasons with high rates of humidity in the forest–steppe region had a stimulating effect on the creation of NPPs. About a half of the total production was contributed by the below–ground component of all three groups of plants (pine trees, shrubs and grasses), so the roots contributed 52% of total NPP in bogs of the middle taiga and forest-steppe,. In contrast, it was 38% in the southern taiga.

The majority of differences in terms of the structure of NPPs were found in moss and shrub production, so the ratios changed in the middle, southern taiga and forest-steppe regions as 1:1.4; 1:1; and 1:2, respectively. The clear trend to increase in NPP values from north to south was found for (i) above–ground component of shrubs and (ii) in a moss (*Sphagnum fuscum*) component, although the contribution of mosses does not differ much from one geographic (or climatic) region to the other. The mosses contribute a large portion of NPP in all studied bog ecosystems in all climatic conditions. Our study revealed that *S. fuscum* makes 32% (232 ± 4 g/m^2/yr) of the total NPP in the middle taiga, 37% (250 ± 30 g/m^2/yr) of the total NPP in the southern taiga, and 29% (257 ± 14 g/m^2/yr) of the total NPP in the forest-steppe region. The presence of *Sphagnum* mosses is one of the main features of bog ecosystems in northern (boreal) regions of Western Siberia. It was of interest to analyze the efficiency of the production process of *Sphagnum* along geographical gradient of its distribution. The relationship between the annual increment of *Sphagnum* growth and the amount of photosynthetically active biomass (i.e., green phytomass) was analyzed in a range of studied ecosystems. The results of regression analysis revealed statistically significant differences in the efficiency of *Sphagnum* mosses in terms of productivity of plants across geographical gradient of their distribution. The efficiency coefficient of the production processes (i.e., production/stock) turned to be 0.5 in the middle taiga, 0.3 in the southern taiga and 0.4 in the forest-steppe. Thus, in the peat–accumulating bogs of Western Siberia, the turnover of the *Sphagnum* moss cover occurs in about two years in the conditions of middle taiga and in three years in the conditions of southern taiga and forest-steppe, which can be considered as one of the factors of ecosystem stability.

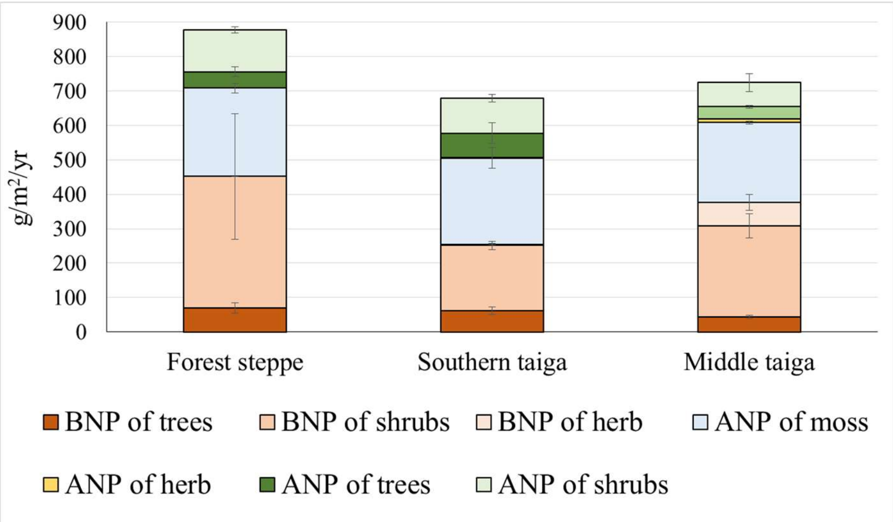

Figure 4. Net Primary Production (NPP), where BNP is below–ground fraction of NPP, and ANP is above–ground fraction of NPP (in g/m^2/yr). The error bars refer to standard deviation (SD).

3.3. Destruction of Plant Organic Matter in Bog Ecosystems

Destruction (or decomposition of plant organic matter) is one of the most important processes in the carbon cycle of wetland/peatland ecosystems. It involves the release of carbon dioxide during the mineralization of peat and plant residues.

In our study, destruction processes were studied for different plant species and different fractions of plant organic matter in bog ecosystems at the same study sites as the studies of production processes in the forest-steppe, as well as in the middle- and southern taiga geographical (climatic) regions. The data are presented in Table 6.

Overall, the rates of destruction processes tend to increase from north to south in Western Siberia. This trend was found for all plant species, all fractions of plant organic matter, and all geographical (climatic) regions in this study, with the only exception for the fraction of stems of shrub species—*Ledum palustre*, that demonstrated the rates of destruction increased in the opposite direction.

The study found the slowest rates of destruction processes for pine tree (*Pinus sylvestris*) residues in all fractions of plant organic matter, but notably in the above–ground component of biomass (the needles and branches). The roots of trees decomposed at some higher rates than that of the above-ground component of tree biomass but remained at the low end among all plant species, although the values are rather comparable with the destruction of below–the ground component (the roots) of *Vaccinium vitis–idaea*. After pine trees, the slow decomposition rates were observed in the moss cover, mainly presented by *Sphagnum fuscum*. It had only slightly different values of decomposition rates in the middle– and southern taiga regions, but somewhat higher values were found in the forest-steppe.

Table 6. Destruction of plant organic matter by different fractions and dominant species of plants, (in % during the first year of decomposition).

Plant Species	Fractions	Middle Taiga	Southern Taiga	Forest Steppe
Pinus sylvestris	needles	6 ± 0.6	7 ± 0.8	10 ± 1.1
	branches	8 ± 0.8	10 ± 0.9	10 ± 1.2
	roots	20 ± 2.1	25 ± 2.6	30 ± 3.1
Andromeda polifolia	leaves	12 ± 1.5	13 ± 1.6	25 ± 2.6
	stems	15 ± 1.6	17 ± 1.8	19 ± 2.1
	roots	21 ± 2.1	27 ± 2.2	35 ± 1.0
Chamaedaphne calyculata	leaves	15 ± 0.5	16 ± 2.1	29 ± 2.5
	stems	15 ± 0.6	17 ± 0.9	19 ± 2.6
	roots	21 ± 2.5	27 ± 2.2	35 ± 1.1
Ledum palustre	leaves	15 ± 0.6	16 ± 1.3	25 ± 1.5
	stems	17 ± 0.5	15 ± 0.9	14 ± 0.9
	roots	21 ± 2.5	27 ± 2.2	35 ± 1.0
Oxycoccus palustris	leaves	15 ± 1.5	16 ± 1.7	20 ± 2.1
	stems	15 ± 0.5	15 ± 0.9	17 ± 1.4
	roots	21 ± 2.5	27 ± 2.2	33 ± 1.2
Vaccinium vitis–idaea	leaves	14 ± 1.6	16 ± 1.7	20 ± 1.8
	stems	12 ± 0.5	14 ± 0.5	15 ± 1.5
	roots	20 ± 2.5	25 ± 2.2	32 ± 1.2
Rubus chamaemorus	leaves	38 ± 0.9	39 ± 0.7	40 ± 0.5
	roots	20 ± 2.2	30 ± 3.1	35 ± 3.2
Sphagnum fuscum		10 ± 0.7	9 ± 0.5	13 ± 0.8
Total plant organic matter, g/m^2/yr		121.5 ± 15.3	132 ± 14.5	213.4 ± 24.5

The study revealed minor differences in the rate of destruction processes among the shrub species. It was found a bit slower for above–ground fractions of *Oxycoccus palustris* and *Vaccinium vitis–idaea* as compared with other species of evergreen shrubs. Very same rates of destruction were found in–the ground fraction of shrub biomass (the roots): it accounted for 21 ± 2.1% in the middle taiga, 27 ± 2.2% in the southern taiga, and 35 ± 1.0% in the forest-steppe regions for all species of shrubs, except for *Vaccinium vitis–idaea*, where the values were 20 ± 2.5, 25 ± 2.2 and 32 ± 1.2%, respectively, for above–mentioned regions. Overall, the stems decomposed more slowly than other parts of the shrubs. The highest rates of decomposition were revealed in the above–ground fraction (leaves) of *Rubus chamaemorus*: it was found to be as much as 38 ± 0.9% in the middle taiga, 39 ± 0.7% in the southern taiga, and 40 ± 0.5% in the forest-steppe regions, that means about a half of leave biomass prone decomposition already in the first year.

Thus, the rate of destruction increased in the following series: *Sphagnum* mosses (10–13%), perennial parts of shrubs (14–17%), tillering nodes and rhizomes of sedges and cotton grass (15–30%), green leaves of grasses and shrubs (12–40%), roots of shrubs (20–40%), rags and fallen leaves of grasses and shrubs (20–40%).

The data on the destruction of plant organic matter are also presented in dry mass, g/m^2/yr, after one year of decomposition in Table 7. In general, the decomposition of plant residues was found at the rate of 121.5 ± 15.3 g/m^2 per year in the middle taiga, and it doubles in the forest-steppe (213.4 ± 24.5 g/m^2 per year).

In the studies of carbon balance, the values of Net Primary Production (NPPs) represent the input– and the values of destruction represent the output components of the carbon budget. In our study, the difference between the input and output of the dry weight of plant organic matter was found in a range of 570 to 656 g/m^2 per year or from 257 to 295 gC/m^2/yr, which represents plant organic matter that enters to peat deposits in the first year. Thus, the overall carbon balance of studied bog ecosystems remains positive.

Table 7. Deposition of plant residues into peat after one year of decomposition, g/m^2 per year (g/m^2/yr) and its standard deviation (±SD). The figures presented in dry organic matter.

Plant Species	Fractions	Middle Taiga	Southern Taiga	Forest Steppe
Pinus sylvestris	needles	25 ± 3	57 ± 11	33 ± 4
	branches	8 ± 1	9 ± 2	9 ± 2
	roots	34 ± 8.5	46 ± 9	48 ± 5
Andromeda polifolia	leaves	4 ± 0.7	1 ± 0.2	6 ± 2
	stems	2 ± 0.5	1 ± 0.1	2 ± 0.4
Chamaedaphne calyculata	leaves	15 ± 1.6	60 ± 5.0	16 ± 2.6
	stems	5 ± 2.1	14 ± 1.7	8 ± 1.1
Ledum palustre	leaves	26 ± 2.7	5 ± 2.3	37 ± 7
	stems	6 ± 1.2	2 ± 0.9	17 ± 4
Oxycoccus palustris	leaves	1 ± 0.5	2 ± 0.4	0
	stems	0	1 ± 0.4	0
Vaccinium vitis-idaea	leaves	1 ± 0.5	1 ± 0.5	6 ± 1.9
	stems	0	0	2 ± 0.6
Total of shrub roots		209 ± 17.5	140 ± 8.4	250 ± 30
Rubus chamaemorus	leaves	7 ± 1.6	1 ± 0.5	0
	roots	54 ± 3.4	3 ± 1.1	0
Sphagnum fuscum		208 ± 21	227 ± 27	224 ± 12
Total		605 ± 45	570 ± 23	656 ± 29
Rate of C accumulation		272 ± 20	257 ± 9	295 ± 13

4. Discussion

The studies of bog ecosystems have shown that despite the relatively similar values of net primary production (NPPs) of pine–dwarf shrub–*Sphagnum* plant communities in the forest-steppe and taiga regions, there are some significant differences found in the structure of live biomass/phytomass. In general, this biomass structure reflects the structure of the plant community, as it was already found in our earlier studies [33,46,57].

Overall, the values of (live and dead) biomass and the Net Primary Production (NPPs), correspond well to some earlier studies in boreal regions of Western Siberia and beyond [5,28,34–36,47,57,59–61]. The dead fraction of biomass (mortmass) predominates in biomass structure across all studied bog ecosystems. Our data revealed no trend in change of biomass values along geographical/climatic gradient. Still, the total (live and dead) biomass was found to be about 40% less in the southern taiga region compared to other regions. The same features were found in the geographical distribution of dead biomass (mortmass).

The study revealed rather minor differences in the values of live biomass (phytomass) across all ecosystems. The lowest values (3508 ± 242) were found in bog ecosystems of the middle taiga, and the highest values (4176 ± 156) were found in bog ecosystems of the southern taiga. About half (40–45%) of the live biomass is contributed by pine trees (*Pinus sylvestris*), of which the main contribution is made by trunks and branches—30%; the tree roots account for about 10%, and the needles account for 4–6%. Among non–tree components, the fraction of live biomass mainly comprises dwarf shrubs.

Also, no geographical gradient was revealed in the spatial distribution of net primary production (NPPs). The bogs in the forest-steppe were found to be the most productive ecosystems in terms of NPPs. About a half of the total production is contributed by below-ground component of all three groups of plants (pine trees, shrubs and grasses)—this high contribution of below–ground NPPs (especially of plants in grasslands, but also in other ecosystems, including wetlands/peatlands) was also found in earlier studies [8,27,57,62–64]. The pine trees make rather minor contributions to NPPs so the majority of NPPs are created by non-wooden components, dwarf shrubs, mosses, and grasses.

Destruction remained a less developed components of carbon cycle research in wetland/peatland ecosystems in Western Siberia and at the global scale. Our study revealed that the rate of destruction tends to increase in the northern and southern regions of Western Siberia. This trend was found for all plant species and all fractions of plant organic matter. Overall, we found our data are in good agreement with a number of previous studies of decomposition of plant organic matter in northern peatlands [23,29–31,65–68]. The plant organic matter decomposed at some slow rates in the northern ecosystems and it is largely constrained by the chemical composition of plants, which contribute to peat formation, as well as environmental conditions, such as temperature and precipitation. For instance, the rate of decomposition of the bogbean plant (*Menyanthes trifoliate* L.) was found to be four times higher than that of the decomposition of *Sphagnum* mosses [23,30,69]. An increase in temperature leads to the enhancement of microbiological activity, and further, it accelerates decomposition processes [70–72]. Also, certain decreases in the water table at the wetland/peatland sites lead to a decrease in the humidity of upper layers of peat deposits, which in turn accelerates the decomposition of plant organic matter. In contrast, with a high water table (under anaerobic conditions), the microbial community is depressed, and the temperature becomes a minor driver of decomposition processes [73,74].

To study the status of bog ecosystems and to measure the carbon balance, i.e., to understand whether the ecosystem represents the sink or the source of carbon, we applied the indicator $B = NPP/D$, where D is the weight of dry organic matter decomposed during the year [50]. However, this B does not consider the loss of carbon through respiration. Across all studied bog ecosystems, the coefficient B varies from 4 to 6, with a minimum value in the forest-steppe, which refers to conditions the most favorable for carbon sequestration, and some higher values (5 and 6) of B found in the southern and the middle taiga regions, respectively. The last could indicate somewhat lower rates of carbon sequestration by ecosystems in the taiga region as compared with the forest–steppe. Our data revealed all bog ecosystems to have a positive carbon balance, then they represent carbon sinks. We suspect, however, the ecosystems of raised bogs could be exposed to progressive drainage under conditions of climate change that constrain peat carbon storage. It intends the wetland/peatland ecosystems to be turned "the source" rather than a sink of atmospheric carbon at some future state of development.

Author Contributions

Conceptualization, A.M.P. and N.P.K.; methodology, N.P.K., N.P.M.-T. and E.K.V.; formal analysis, E.K.V., N.G.K., V.A.S.; investigation, A.M.P., N.P.K., N.P.M.-T., E.K.V., N.G.K., V.A.S., S.S.K.; resources, N.P.M.-T.; writing—original draft preparation, N.P.K., A.M.P.; writing—review & editing, N.P.K., A.M.P., E.K.V., S.S.K.; Visualization, A.M.P., N.P.K. All authors have read and agreed to the published version of the manuscript.

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