

Above- and below-ground phytomass and net primary production in boreal mire ecosystems of Western Siberia

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Abstract We measured phytomass stock and production in Western Siberian mire ecosystems (palsa, ridge, oligotrophic and mesotrophic hollows, fen). To determine the contribution of different phytomass fractions into total production, we developed a method to estimate below-ground production (BNP). Standing crop of living above-ground phytomass on treeless plots varied from 300 to 660 g m⁻², reaching maximum on palsa, where 81% of phytomass consisted of *Sphagnum* mosses and lichens. In the hollows and the fen, *Sphagnum* percentage varied from 70 to 95%. Standing crop of living below-ground phytomass varied from 325 to 1,210 g m⁻². It consisted of woody stems, stem bases, rhizomes and roots, with the latter contributing from 30 to 60%. Total production of mire ecosystems in northern taiga of Western Siberia ranged from 350 to 960 g m⁻² year⁻¹ and depended on microtopography of the ecosystem (the presence of permafrost and water table depth). Production of treeless plant communities located on the elevated sites depended on the presence of permafrost: in comparison with the ridge, palsa production was lower. Production on the low sites increased with increase pH and reached maximum (960 g m⁻² year⁻¹) in poor fens. Bryophytes were the major producers

above ground. Their production varied from 100 to 272 g m⁻² year⁻¹ and reached maximum on ridges. BNP contributed 37–66%, increasing due to increased contribution of sedges.

Keywords Mire ecosystems · Standing phytomass · *Sphagnum* mosses · Above-ground production · Below-ground production · Western Siberia

Introduction

The total amount of C stored in soils of the world is estimated as $1,477 \times 10^{15}$ g C, whereas the amount of C stored in peat is estimated to reach 270–450 × 10¹⁵ g C (Gorham 1991; Turunen et al. 2002), or about 30% of the global soil organic carbon pool. Western Siberian peatlands are estimated to account for about 40% of the global peat deposits (Walter 1977). Boreal peatlands may be considerably affected by changes in climate and land use (IPCC 1995; Alm et al. 2001). However, models of global carbon budget that have been developed so far use little information about Siberia. To simulate explicitly the role of Siberian peatlands in the global carbon cycle, it is essential to know the area of mires in Western Siberia, their carbon store, as well as net primary production (NPP) and decomposition rates of dead plant matter in different types of peatlands. These data will allow estimating net peat accumulation because it is calculated as NPP minus total

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decomposition, of both fresh and old organic matter, through the peat column.

The area of Western Siberian peatlands is 1.02×10^6 km², or 8% of the global wetlands, with the total amount of peat stored estimated as 111.3 Gt, or 0.55 Gt of organic carbon (Yefremov and Yefremova 2001). The northern taiga subzone of Western Siberia, where this study was carried out, has peatland area of 22.6×10^3 km², storing 20.8 Gt of peat, and 10.2 Gt of organic carbon.

It is impossible yet to estimate NPP and organic matter decomposition for the total area of Western Siberian wetlands for two reasons: high diversity of mire types characterized by specific rates of decomposition and production, the scarcity of above-ground production (ANP) estimates, and the absence of estimates of below-ground production (BNP) and organic matter decomposition.

For the boreal Western Siberia the estimates of phytomass production are available only for the southern taiga, where raised bogs, transitional mires, and poor fens were studied. The NPP rates of these mire ecosystems varied little (330–360 g m⁻² year⁻¹) and the share of below-ground phytomass production did not exceed 20% (Bazilevich 1993).

Estimation of BNP is a complicated task, especially in peatlands, but it should be addressed since in terrestrial ecosystems a substantial part of primary production is allocated below-ground, accounting for 15–90% of the total annual production (Coleman 1976; Aerts et al. 1992; Titlyanova et al. 1999). In recent years several studies showed that also in peatlands most of the assimilated carbon is continuously translocated to the below-ground biomass of vascular plants (Wallén 1986, 1992; Saarinen 1996; Grogan and Chapin III 2000; Moore et al. 2002).

The aim of our work was to estimate total primary production, both above- and below-ground, for the major types of mires in the northern taiga of Western Siberia, developing and using a method to estimate BNP in peatlands.

Materials and methods

Study sites

The study sites were located in mires of the northern taiga subzone of Western Siberia near the town

Noyabrsk (63°30' N, 78°20' E) (Fig. 1). The large lowlands of this region are covered by 1–3 m thick peat layer (Yefremov and Yefremova 2001).

The mean annual temperature is -4.4°C , with extremes from -21.8°C to $+17.0^\circ\text{C}$ in January (the coldest month) and July (the warmest month), respectively. The mean annual precipitation is 454 mm and varies widely. The frost-free period is usually 70–100 days, and snow cover stays for about 220 days (Reference book on climate of the USSR 1972).

The study sites were located on the territory of the so called Siberian Hills, which according to the geomorphological zoning of West Siberia (Arkhipov et al. 1970) represent flat or low-hill plane. The altitudes in the northern taiga there vary from 110 to 160 m above sea level, whereas the height of the hills varies from 30 to 50 m. Mires are mostly located on flat or low-hill areas. Permafrost palsa mires are commonly located on the watershed 146 m above sea level. The area is drained by small rivers and rivulets with little floodplains and low terraces, where in valleys mesotrophic sedge mires are common. The southern macroslope of the Siberian Hills is covered by ridge-hollow mires (Arkhipov et al. 1970).

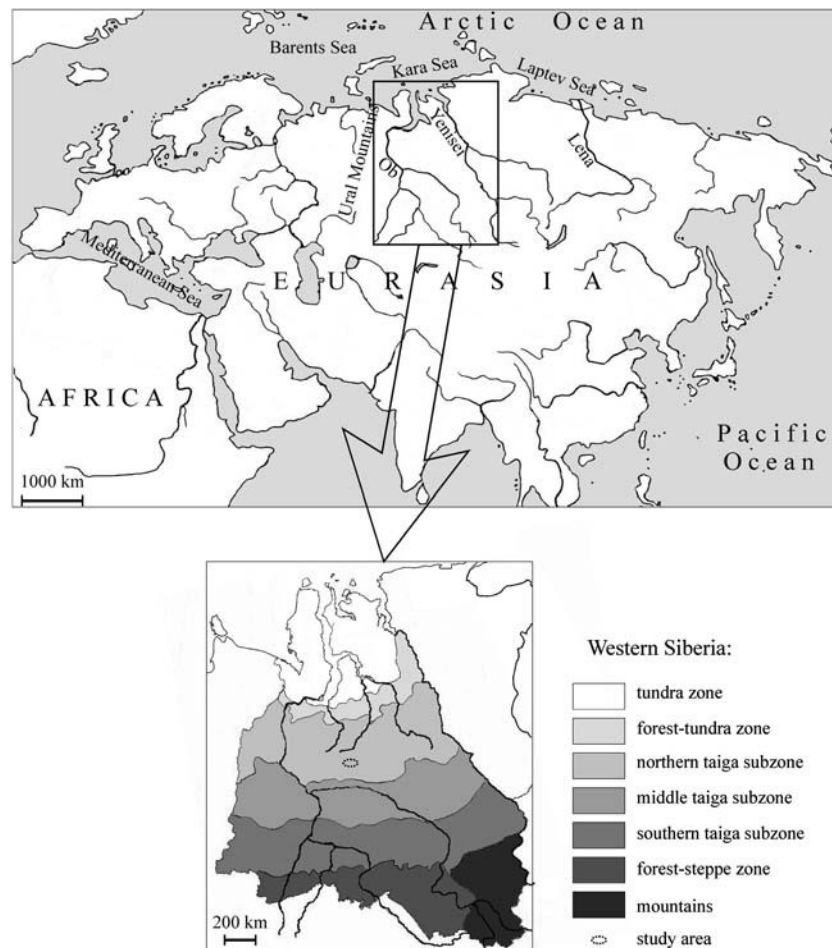
More than 60% of peatlands consist of flat palsa mires with discontinuous permafrost and ridge-hollow-pool complexes (Vasiliev and Peregon 2001). Flat palsa mires consist of ridges with permafrost palsa and waterlogged hollows. Palsas are covered by shrubs, mosses and lichens, whereas hollows are covered mainly by sedges and *Sphagnum*.

Oligotrophic bogs occupy vast watershed areas. Bog slopes usually are better drained, have ridges alternating with hollows, usually covered by *Sphagnum* and *Carex* species. The wide segments of river valleys can be occupied by treeless or sparsely wooded minerotrophic fens (Semenova and Lapshina 2001).

We use the terms oligotrophic and mesotrophic ecosystem to classify mire ecosystems determined by the composition of plant species having the different demand (low or medium) for nutrients.

We studied five sites during 1998–2000: a palsa and an oligotrophic hollow in the flat-palsa mire, an oligotrophic unfrozen ridge and a mesotrophic hollow in the ridge-hollow-pool complex, and a mesotrophic fen in a small river valley. Additionally, in 2000 we

Fig. 1 Location of the study region



studied a palsa mire and an oligotrophic hollow, dominated by *Sphagnum*, on the edge of the big mire. On the palsa we studied two types of microrelief elements: randomly distributed irregularly shaped small hummocks dominated by lichens and *Sphagnum*, and lawns between hummocks completely dominated by lichens. Some study site characteristics are given in Table 1 and Fig. 2.

The chosen study sites differ in relief, peat thickness, and vegetation. Interspals and interridge hollows are more similar in ecological conditions and vegetation types, than the elevated elements of the same mire, i.e., palsa and ridge. Therefore, further on we refer to palsas and ridges as the high sites, and hollows and fens as the low sites.

On palsa and ridges there were trees, their number was 150 ind. ha⁻¹ on palsa and 1,300 ind. ha⁻¹ on ridges. Low sites were treeless (Table 1).

Estimation of above- and below-ground net primary production

To estimate total NPP in mires we distinguished the following vegetation fractions: above-ground herbs, shrubs, dwarf shrubs, *Sphagnum* mosses and lichens, as well as stem bases (SB), rhizomes, roots of herbs and shrubs.

In order to estimate the phytomass and production of those fractions, we set up sample plots (100 m²) on each study site. From each plot, 10 samples were taken in June, July, and September. The phytomass of herbs, shrubs and dwarf shrubs was clipped above the surface of mosses from quadrates of 0.25 m². Stems, stem bases, rhizomes, roots of herbs, sedges, herbs, shrubs, and dwarf shrubs located below the clipping plane, were considered below-ground phytomass. We took the living bryophytes below the clipping line as

Table 1 Some characteristics of study sites

Mire type	Flat-palsa mire			Ridge-hollow-pool mire			Minerotrophic fen	
	Palsa	Hollow	Ridge	Ridge	Hollow	Hollow	Poor fen	Mesotrophic
Mire ecosystem	Oligotrophic	Oligotrophic	Oligotrophic	Oligotrophic	Mesotrophic	Mesotrophic	Poor fen	Mesotrophic
Kind of ecosystem	30–35 cm below the surface	–	–	–	–	–	–	–
Permafrost	–	5–10	35–40	35–40	5–10	5–10	10–20	10–20
Depth of water table, m	–	–	0.5–1.2	0.5–1.2	–	–	–	1.3
Peat thickness, m	1.4–1.6	–	–	–	–	–	–	–
Vegetation	<i>Pinus sylvestris</i> L.	–	<i>Pinus sylvestris</i> L., <i>Betula pubescens</i> Ehrh.	–	–	–	–	–
Trees	–	–	–	–	–	–	–	–
Shrubs and dwarf shrubs	<i>Ledum palustre</i> L., <i>Betula nana</i> L., <i>Vaccinium vitis-idaea</i> L., <i>Vaccinium uliginosum</i> L., <i>Andromeda polifolia</i> L., <i>Oxycoccus microcarpus</i> Turez. ex Rupr.	<i>Oxycoccus palustris</i> Pers., <i>Andromeda polifolia</i> L.	<i>Ledum palustre</i> L., <i>Betula nana</i> L., <i>Vaccinium vitis-idaea</i> L., <i>Vaccinium uliginosum</i> L., <i>Andromeda polifolia</i> L., <i>Oxycoccus microcarpus</i> Turez. ex Rupr.	<i>Ledum palustre</i> L., <i>Betula nana</i> L., <i>Vaccinium vitis-idaea</i> L., <i>Vaccinium uliginosum</i> L., <i>Andromeda polifolia</i> L., <i>Oxycoccus microcarpus</i> Turez. ex Rupr.	<i>Andromeda polifolia</i> L., <i>Oxycoccus palustris</i> Pers.	<i>Andromeda polifolia</i> L., <i>Oxycoccus palustris</i> Pers.	<i>Oxycoccus palustris</i> Pers., <i>Andromeda polifolia</i> L.	<i>Oxycoccus palustris</i> Pers., <i>Andromeda polifolia</i> L.
Herbs	<i>Rubus chamaemorus</i> L.	<i>Carex limosa</i> L.	<i>Rubus chamaemorus</i> L.	<i>Rubus chamaemorus</i> L.	<i>Carex rostrata</i> Stokes, <i>Carex chondrorrhiza</i> Ehrh., <i>Carex limosa</i> L.	<i>Carex rostrata</i> Stokes, <i>Carex chondrorrhiza</i> Ehrh., <i>Carex limosa</i> L.	<i>Carex rostrata</i> Stokes, <i>Carex limosa</i> L.	<i>Carex rostrata</i> Stokes, <i>Carex limosa</i> L.
Mosses	<i>Sphagnum fuscum</i> (Schimp.) Klinggr.	<i>Sphagnum lindbergii</i> Schimp. ex Lindb., <i>Sphagnum teres</i> (Schimp.) Aongstr. ex Hartn	<i>Sphagnum fuscum</i> (Schimp.) Klinggr.	<i>Sphagnum fuscum</i> (Schimp.) Klinggr.	<i>Sphagnum fuscum</i> (Schimp.) Klinggr.	<i>Sphagnum majus</i> (Russ.) C.Jens.	<i>Sphagnum riparium</i> Aongst.	<i>Sphagnum riparium</i> Aongst.
Lichens	<i>Cladina rangiferina</i> (L.) Harm., <i>Cladina stellaris</i> (Opiz) Brodo	–	<i>Cladina rangiferina</i> (L.) Harm., <i>Cladina stellaris</i> (Opiz) Brodo	<i>Cladina rangiferina</i> (L.) Harm., <i>Cladina stellaris</i> (Opiz) Brodo	–	–	–	–



Fig. 2 Schematic presentation of microrelief of the study sites

contributing to above-ground phytomass. We took other samples (1 dm^3) to measure the phytomass of bryophytes in the above-ground layer and below-ground phytomass. On the same quadrats where above-ground phytomass was clipped, we sampled below-ground phytomass in 10-cm depth increments to 30 cm below the moss surface. All fresh samples were sorted into the appropriate fractions.

We measured the living above-ground phytomass as consisting of the following fractions: green parts of herbs; living shrub leaves of the current and the previous year; current year and perennial shoots, woody parts located above the clipping plane; green parts of mosses or, for red and brown mosses, the upper part of shoots till the dark line, which separates the stem and the branches formed in the previous years; photosynthesizing upper parts of lichen stems with branches, which differ from the main podetia by its brighter-green colour.

Above-ground production

Above-ground production of herbs was taken as equal to the seasonally maximal standing green phytomass, ANP_H . We estimated the production of deciduous shrubs as a sum of the seasonal maximum of green leaves phytomass and young shoots of the current year, ANP_{S1} . We calculated the production of evergreen shrubs as a maximal phytomass of the current year' shoots plus their leaves, ANP_{S2} . Production of perennial shrub parts was calculated by dividing their phytomass by the number of rings in the basal part of the stems.

Production of lichens was estimated as a difference between seasonal maximum and minimum of green phytomass, ANP_L . We took into account the basal lichen cover to estimate ANP_L per 1 m^2 . *Sphagnum* mosses production was estimated taking into account the measurements of the basal cover, in percent, linear shoot growth rate (mm), shoot density (no dm^{-2}) and specific shoot mass/length

relationship. We could not use the cranked-wire method (Clymo 1970) to estimate shoot growth, as wires were sinking in hollows. Since thread method can cause stem deformation, we modified it by using individual tags, which allowed us to avoid affecting linear growth of shoots.

We attached thin wire rings immediately below the capitulum of a moss. A label of aluminium foil was put on the other end of the wire, which was 5–10 cm from the plant, in such a way as to ensure that the wire ring did not damage the stem. Such wire rings were put on 70–100 plants on each study site. The tagged plants were sampled the next year. For every sample linear shoot growth was estimated as the distance between the level immediately below the capitulum of the plant the next year and the original level where the ring stayed. The grown part of the stem was cut off, dried and weighed to estimate the yearly growth rate of the moss. Every labelled sample was picked out from a 100 cm^2 plot. Shoot density was also determined on those plots. Production of every *Sphagnum* species was equal to the mean annual increment of one shoot multiplied by shoot density. The sum of thus estimated annual increments of different species corrected for their basal cover gave the annual production of mosses, ANP_M .

Thus, for a community as a whole the total annual ANP is given by equation:

$$\text{ANP} = \text{ANP}_H + \text{ANP}_{S1} + \text{ANP}_{S2} + \text{ANP}_L + \text{ANP}_M$$

Below-ground production

We developed a method to estimate BNP, taking into account the fractions of stem bases, rhizomes and roots, growing during the current year.

Stem bases were divided into two groups: young (grown up during the current year) and the old. Young stem bases had many young roots, that were more light in colour and came directly from stems. Their phytomass was taken as equal to their production. Rhizomes were also divided into young and old ones. The current year rhizomes are lighter in colour than old ones and have vegetative shoots on top. Their mass is taken as equal to their production.

Roots are divided into groups according to their age which is indicated by some morphological characteristics, such as root colour, diameter, degree

of lateral ramification, positioning on below-ground rhizomes and first-order roots. Roots of herbs and sedges (RH) were sorted into four easily distinguishable groups. Roots H₁ grow during early spring, are small in number, do not have any second- and third-order roots and are connected to the young shoots of the current year. Roots-H₁ of *Carex* are characterized by the largest diameter and light colour due to the presence of living rhizoderm with living root hairs and living primary cortex. Roots H₁ of *Eriophorum* genus are characterized by light pink or purplish colour. The phytomass of roots H₁(R-H₁) comprises a portion of BNP.

Roots H₂ are branching appendicular roots and darker coloured. They are attached to the bases of those stems that formed during the previous fall and became generative ones during the current summer. These roots are 20–40 cm long. Among them the roots of *Carex* can be easily distinguished due to their large number of light-coloured appendicular second- and third-order roots. The phytomass R-H₂ contributes to BNP.

Roots H₃ are dark-coloured branching appendicular roots attached to the dead parts of generative shoots. These are rigid roots with no apical growth and no lateral roots which former presence is indicated by scars. Roots H₃ (R-H₃), comprising a fraction of the living roots phytomass, are not taken into account to as contributing to BNP of the current year.

Dead below-ground organs: roots-H₄, rhizomes and stem bases. Roots H₄ are non-ramifying, dark-coloured and partly decomposed, having no second- and third-order roots due to destruction. These roots could have died off last year or a few years ago. They usually are not connected to the living plant organs, or are easily broken off of the latter with the break-off surface coloured dark grey.

The roots of shrubs and dwarf shrubs, RS, are divided into three groups. Roots S₁ are fine roots of the current year, 0.1–1 mm in diameter, growing from the parts of shrub stems that are surrounded by moss, or being the last order of ramification. Fine roots have specific colour varying from light pink to light brown and are flexible and tender. The finest roots of this fraction are abundant in the upper layer of mosses, concentrating around moss stems. The longevity of the fine roots ranges from a few days to a few months. During hot summer time they might die-off, and reappear at the end of the season. The RS₁ phytomass also contributes into BNP.

Roots S₂ are living roots grown during the previous year, having similar to roots S₁ diameter, but much darker epidermis. Roots S₃ are living roots with diameter exceeding 1 mm and aged over 1 year. The RS₂ and RS₃ roots, comprising a fraction of below-ground phytomass, are not taken into account for estimating BNP.

Thus, BNP is determined as a sum of stem bases, rhizomes and roots phytomass grown during the current season:

$$\text{BNP} = \text{SB} + \text{Rh} + \text{RH}_1 + \text{RH}_2 + \text{RS}_1$$

Then total production is $\text{NPP} = \text{ANP} + \text{BNP}$.

Statistical analysis of the data

We analyzed the data by performing ANOVA, multi-dimensional scaling and principal components analysis of the log-transformed data using Statistica v.5.5.

Results

Standing crop of living phytomass

Standing crop of living above-ground phytomass on treeless plots varied from 290 to 660 g m⁻² (Table 2), reaching maximum on palsa, where 81% of living phytomass consisted of mosses and lichen. Standing crop of living phytomass decreased on ridges as a result of the decrease in lichens phytomass, but was still higher than in the hollows. In the hollows and fens, *Sphagnum* made up 70–95% of standing crop, which totalled 290–470 g m⁻².

The above-ground phytomass of vascular plants in the investigated mire ecosystems was shown to reach maximum on ridges, where perennial parts of shrubs and dwarf shrubs contributed 60% into it, and minimum in oligotrophic hollows. In hollows, the phytomass of vascular plants was formed mainly by sedges and herbs. In fens the percentage of dwarf shrubs in the standing crop was similar to that of herbs vegetation (Table 2).

Living below-ground phytomass was higher than above-ground phytomass in most cases (Table 2). The mesotrophic hollow was characterized by three-fold difference in above- and below-ground phytomass, whereas in the oligotrophic hollow the

Table 2 Total phytomass in the mire ecosystems (g d.w. m⁻²) averaged over 3 growing seasons

Phytomass fractions	High sites		Low sites		
	Palsa	Ridge	Hollows in complex with		River valley poor fen
	Oligotrophic		Palsa	Ridge	Mesotrophic
	Oligotrophic		Oligotrophic	Mesotrophic	Mesotrophic
<i>Above-ground phytomass</i>					
Shrubs and dwarf shrubs:					
Green parts	54 ± 7	98 ± 9	1 ± 1	7 ± 2	29 ± 3
Perennial parts	59 ± 8	163 ± 16	1 ± 1	7 ± 1	23 ± 4
Herbs, green	9 ± 3	6 ± 0.3	13 ± 2	74 ± 10	43 ± 6
Green mosses	1 ± 0.1	8 ± 1	–	–	–
Sphagnum	290 ± 55	341 ± 31	310 ± 18	200 ± 20	371 ± 21
Lichens	245 ± 52	4 ± 0.2	–	–	–
Total above-ground phytomass	658 ± 44 d*	620 ± 21 d	325 ± 10 b	288 ± 13 a	466 ± 13 c
<i>Below-ground phytomass</i>					
Woody stems in the 0–30 cm layer	327 ± 23	605 ± 43	3 ± 2	10 ± 0.6	131 ± 11
Stem bases, rhizomes and roots in the layer:					
0–10 cm	131 ± 21	194 ± 21	231 ± 20	483 ± 88	44 ± 7
10–20 cm	204 ± 22	218 ± 22	78 ± 9	345 ± 54	445 ± 71
20–30 cm	155 ± 25	193 ± 19	13 ± 1	148 ± 20	253 ± 30
Total below-ground phytomass in 0–30 cm	817 ± 26 b	1210 ± 32 d	325 ± 13 a	986 ± 61 c	873 ± 45 bc
Total phytomass	1475 ± 30 c	1830 ± 22 d	650 ± 9 a	1274 ± 36 b	1339 ± 27 b

*Values in rows followed by different letters, differ significantly at $P < 0.05$ level

values were the same. In the hollows 50–70% of the living below-ground phytomass was concentrated in 0–10 cm layer, whereas on the high sites most of the roots and rhizomes phytomass was concentrated in the 10–30 cm layer.

Below-ground phytomass composition differed among various study sites (Table 2). On the high sites, the phytomass consisted of woody stems of shrubs and dwarf shrubs, and roots. In the hollows 35–60% of plant material consisted of stem bases and rhizomes. Stem bases accounted for half of the below-ground phytomass in the fen. The contribution of roots into below-ground phytomass ranged from 30 to 60%, reaching maximum in the oligotrophic hollow. Total phytomass was maximal on the high sites, where 55–65% were contributed by the below-ground phytomass. Total phytomass decreased in the mesotrophic hollow where the contribution of below-ground phytomass increased to 77%, and reached minimum in the oligotrophic hollow, where above- and below-ground fractions contributed equally into the total phytomass.

Production

Production of mosses

Linear growth rate of mosses in mire ecosystems of northern taiga varied from 5 to 60 mm a season, depending on moss species and its habitat (Table 3). Linear growth rate of *Sphagnum fuscum*, which dominated the high sites, was four times lower on the palsa in comparison with the ridge. At the same time, its density was much higher on the palsa, leading to no difference in their production between the sites. *Sphagnum nemoreum*, growing in small patches on the ridges, had somewhat slower rate of linear growth and significantly less density in comparison with *S. fuscum*, which resulted in its minimal production among all species. *Sphagnum linbergii* dominated the moss cover in the oligotrophic hollow. Its production rate was similar to that of the mosses, inhabiting the palsa and the ridge. In comparison with the dominant *S. linbergii*, co-dominant *S. balticum* had somewhat more intensive linear growth and

Table 3 Some production characteristics of *Sphagnum* populations in different study sites (mean \pm sem)

Species	Site	Coverage, %	Linear growth, mm	Density, ind. dm ⁻²	Production, g dm ⁻² year ⁻¹	Production, g m ⁻² year ⁻¹
<i>Sphagnum fuscum</i> (Schimp.) Klinggr.	P	50	5 \pm 1 a*	900 \pm 90 g	1.8 \pm 0.2 a	90**
<i>Sphagnum fuscum</i> (Schimp.) Klinggr.	R	90	20 \pm 5 b	640 \pm 50 f	2.2 \pm 0.3 a	198
<i>Sphagnum nemoreum</i> Scop.	R	1	15 \pm 5 b	408 \pm 40 e	1.5 \pm 0.2 a	1.5
<i>Sphagnum lindbergii</i> Schimp. ex Lindb.	OH	100	23 \pm 2 b	126 \pm 9 cd	2.2 \pm 0.2 a	220
<i>Sphagnum balticum</i> (Russ.) Russ. ex C.Jens.	OH	50	30 \pm 3 b	106 \pm 8 bc	3.0 \pm 0.1 b	150
<i>Sphagnum majus</i> (Russ.) C.Jens.	MH	80	60 \pm 3 c	96 \pm 5 b	2.0 \pm 0.2 a	160
<i>Sphagnum compactum</i> DC. in Lam. et DC.	MH	1	20 \pm 2 b	44 \pm 10 a	2.1 \pm 0.2 a	2.1
<i>Sphagnum riparium</i> Aongst.	Fen	90	61 \pm 6 c	147 \pm 10 d	2.5 \pm 0.2 a	225

* Values in columns followed by different letters, differ significantly at $P < 0.05$ level

** Values in the column are counted with recalculation on a plant coverage

hence the biggest production among eight investigated species. The linear growth rate of *S. majus*, dominating in the mesotrophic hollow, reached 60 mm a season, which was 4.6 times higher than average and two times higher than the growth of mosses in the oligotrophic hollows. *Sphagnum compactum* inhabited the mesotrophic hollow in scarce patches together with *S. majus*. Production of *S. riparium*, dominating in poor fens, was similar to that of *S. compactum* and *S. majus*. Production of *S. riparium*, dominating in poor fens, was equal to that of *S. compactum* and *S. majus*.

Overall, linear growth of mosses increased, and density decreased in the series of ecosystems from the palsa to the poor fen. Compared to the highest values, the minimal estimates of linear growth rate and plant density were 8% and 5%, respectively. As estimation of production depends on linear growth and density, its rate ranged 1.5–3.0 g dm⁻² year⁻¹, i.e., differed only twofold.

Figure 3 shows location of population characteristics of *Sphagnum* species of study sites in the plane of the first two principal components, accounting for 52% and 32% of the total variance, respectively. The first principal component distinguishes clearly the high sites, i.e., palsa and ridge, which are in the positive semiplane, from the low sites in the negative semiplane, and correlates positively with population density (0.79) and negatively with production (–0.81) and linear growth (–0.88). The second principal component distinguishes different species growing in one and the same study sites, and therefore can be attributed to biological peculiarities of species.

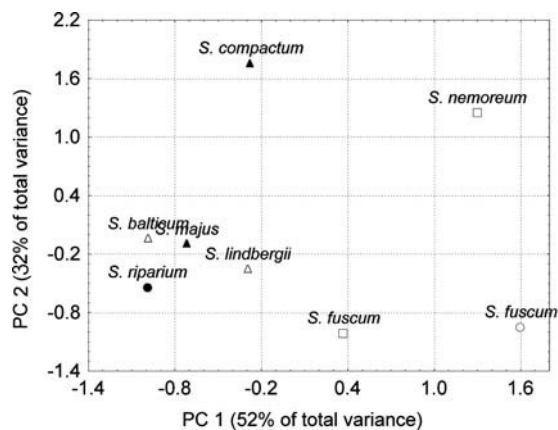


Fig. 3 Location of different *Sphagnum* populations in different study sites (factor scores) in the plane of principal components 1 and 2. ○—palsa, □—ridge, △—oligotrophic hollow, ▲—mesotrophic hollow, and ●—fen

Total production

The total production (NPP) in the study sites in peatland ecosystems of northern taiga subzone of Western Siberia varied from 350 to 960 g m⁻² year⁻¹, depending on ecosystem topography and degree of nutrient provision of plants (Table 4). Production of treeless plant communities on the high sites did not differ significantly. Production of the hollows and the fen increased from 350 g m⁻² year⁻¹ in oligotrophic hollows to 960 g m⁻² year⁻¹ in the poor fen, with increasing pH of bog water.

Differences between the study sites were most evident in the contribution of vascular plants and bryophytes together with lichens to the ANP and of

Table 4 NPP of mire ecosystems in northern taiga, $\text{g m}^{-2} \text{ year}^{-1}$ (mean \pm sem)

	ANP				BNP	Total production
	Herbs	Shrubs and dwarf shrubs	Bryophytes and lichens	Total		
<i>Palsa</i>						
1998	4 \pm 2	54 \pm 11	179 \pm 20	237 \pm 69	322 \pm 35	557 \pm 113
1999	16 \pm 2	53 \pm 16	200 \pm 14	269 \pm 61	194 \pm 29	463 \pm 108
2000	15 \pm 9	66 \pm 7	214 \pm 11	295 \pm 49	363 \pm 27	658 \pm 307
Mean	12 \pm 4 a*	58 \pm 4 b	198 \pm 10 a	267 \pm 17 ab	293 \pm 21 b	559 \pm 56 b
<i>Ridge</i>						
1998	2 \pm 0.6	121 \pm 6	216 \pm 40	339 \pm 76	275 \pm 22	614 \pm 172
1999	5 \pm 0.3	112 \pm 4	242 \pm 30	359 \pm 56	216 \pm 12	575 \pm 136
2000	13 \pm 1	153 \pm 7	376 \pm 80	542 \pm 101	226 \pm 19	768 \pm 169
Mean	7 \pm 3 a	129 \pm 12 c	278 \pm 50 a	414 \pm 65 b	239 \pm 18 b	653 \pm 59 b
<i>Oligotrophic hollow</i>						
1998	14 \pm 0.5	0	181 \pm 18	195 \pm 18	160 \pm 19	355 \pm 117
1999	9 \pm 1	0	148 \pm 33	157 \pm 33	160 \pm 18	317 \pm 98
2000	21 \pm 0.6	0	260 \pm 67	281 \pm 67	110 \pm 3	391 \pm 79
Mean	15 \pm 3 a	0 a	196 \pm 33 a	211 \pm 37 a	143 \pm 17 a	354 \pm 21 a
<i>Mesotrophic hollow</i>						
1998	53 \pm 4	2	200 \pm 45	255 \pm 55	409 \pm 49	664 \pm 350
1999	80 \pm 2	2	250 \pm 98	332 \pm 101	358 \pm 32	688 \pm 341
2000	86 \pm 5	2	202 \pm 40	290 \pm 57	448 \pm 33	736 \pm 238
Mean	73 \pm 10 b	2 a	217 \pm 16 ab	292 \pm 22 a	405 \pm 26 bc	697 \pm 21 b
<i>Poor fen</i>						
1998	43 \pm 1	28 \pm 2	240 \pm 26	311 \pm 31	797 \pm 49	1108 \pm 394
1999	73 \pm 4	34 \pm 1	197 \pm 39	304 \pm 52	689 \pm 38	993 \pm 311
2000	78 \pm 4	9 \pm 2	270 \pm 50	357 \pm 60	415 \pm 48	772 \pm 343
Mean	65 \pm 11 b	24 \pm 8 b	236 \pm 21 ab	324 \pm 17 ab	634 \pm 114 c	959 \pm 99 c

*Values in columns followed by different letters, differ significantly at $P < 0.05$ level

the BNP to total NPP (Table 4). The ANP of vascular plants accounted for 26% of total ANP on the palsa, 33% on the ridge, 7% in the oligotrophic and 25% in the mesotrophic hollows, and 27% in the poor fen. On the high sites 80–95% of vascular plants ANP were provided by shrubs and dwarf shrubs, in hollows 98–100%—by herbs, in fens 27% were provided by shrubs and dwarf shrubs and 73% by herbs.

Above-ground production of bryophytes and lichens ranged within 200–300 $\text{g m}^{-2} \text{ year}^{-1}$. Its changes from year to year were much lower compared to that of other species (Table 4). Production of bryophytes was minimal on the palsa and in the oligotrophic hollow. Mosses production reached maximum on the ridge, where it increased to 380 $\text{g m}^{-2} \text{ year}^{-1}$ in a wet year 2000. The contribution

of bryophytes and lichens into ANP changed from 67% on the ridges to 93% in the oligotrophic hollow. So bryophytes and lichens were shown to be the major producers of the above-ground layer.

The estimates of BNP value and its contribution into total NPP strongly differed among the studied ecosystems (Table 4). The BNP estimate was minimal in the oligotrophic hollow, where standing crop of vascular plants did not exceed 15 $\text{g m}^{-2} \text{ year}^{-1}$, and maximal in the poor fen mainly due to stem bases growth. The BNP contribution into the ecosystem NPP accounted for 37–66%; on the palsas, mesotrophic hollow and fen exceeding the ANP value. The BNP on the palsa and the ridge did not differ significantly. In the mesotrophic hollow and the fen the increase in BNP most likely resulted from

the increase in species abundance of herbs and sedges.

The year-to-year changes in NPP, as observed over the 3-year period, could overcome differences among three ecosystems: the palsa, the ridge and the mesotrophic hollow. The oligotrophic hollow produced minimal, whereas the fen produced maximal phytomass among the studied ecosystems over the period of investigation.

Figure 4 shows location of different study sites obtained by multi-dimensional scaling of the data. Dimension one clearly separates the high and relatively dry sites from low and wetter ones. Dimension two separates low sites according to plant demand for nutrients. Thus, phytomass standing crop in northern taiga seems to be governed by the water table depth and degree of nutrient supply to plants.

Discussion

Standing crop of living phytomass

Bryophytes are the edificators in mire ecosystems of the northern taiga and create specific conditions of nearby environment for vascular plants. Mosses are the main peat-forming plants which hold the water and acidify the surroundings. According to Bazilevich (1993), the living phytomass of bryophytes + lichens in Russian boreal mires ranges 190–840 g m⁻² and depends mostly on mire type, rather than on climatic conditions. Ombrotrophic bogs are characterized by the high phytomass of bryophytes. The data obtained in our study fell within the indicated

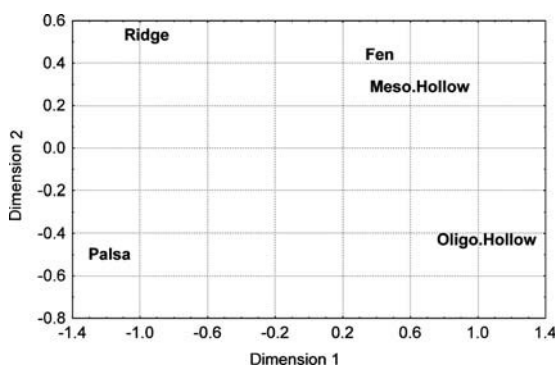


Fig. 4 Three-dimensional scaling of study sites according to their standing phytomass. P—palsa, R—ridge, OH—oligotrophic hollow, MH—mesotrophic hollow, and F—fen

range and varied from 56 to 95% of the total above-ground phytomass (Table 2).

Thus, in northern mires, the composition of above-ground phytomass was mainly influenced by topography: the high and relatively dry oligotrophic sites were much more favourable for the development of dwarf shrubs and shrubs due to favourable hydrologic conditions, whereas mesotrophic hollows mostly favoured sedges and herbs. The similar difference between hummock and hollow sites was shown in the mire systems of Sweden, Finland, and Canada (Backēus 1985, Moore et al. 2002).

There is a clear relationship between the standing crop of vascular plants phytomass and ecosystem temperature: the warmer the environment is, the higher is the standing crop (Backēus 1985; Bazilevich 1993; Kosykh et al. 2003). Within the same climatic zone water regime plays the most important role: on hummocks the vascular plants' phytomass is usually higher, and the more so on the high hummocks in comparison with the low ones (Vasander 1981; Backēus 1985).

The estimates of below-ground phytomass, including woody shoots of shrubs and dwarf shrubs submerged into the moss layer, were either similar to or exceeded the above-ground phytomass. However, the living roots phytomass is rather small and lower than the above-ground phytomass. There is a functional relationship between green photosynthesizing organs and roots: the phytomass of roots should be sufficient to provide photosynthesizing phytomass with water and nutrient elements; reciprocally, photosynthesizing phytomass should be able to provide roots with photoassimilates. This relationship is not linear and depends on species composition and edaphic conditions of plant growth (Fig. 5). The

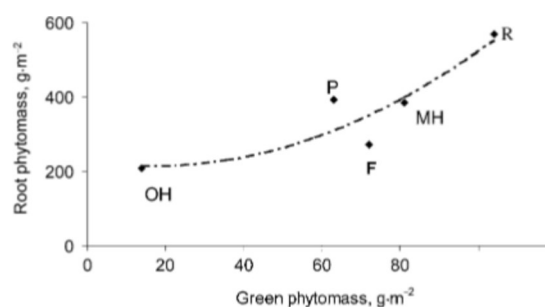


Fig. 5 Relationship between green and root phytomass. P—palsa, R—ridge, OH—oligotrophic hollow, MH—mesotrophic hollow, and F—fen

greater is the deficit of water, oxygen and nutrients, the higher is the ratio R/G, where R is living root phytomass, and G is the photosynthesizing phytomass (Titlyanova 1977).

On the elevated sites, where G is formed mainly by shrubs, the ratio R/G is estimated to be 8.2 and 5.5 higher than on the palsa, where permafrost is the major stressor impeding the warming of peat layers. With decrease in plant nutrients availability in depressed sites (Bleuten 2001), the values of R/G increased, being 3.8 in the fen, 4.7 in the mesotrophic hollow, and 14.3 in the oligotrophic hollow (Fig. 5).

In literature there are little data on below-ground living phytomass in mire ecosystems because of lack of a reliable method to estimate it (Wallén 1992). Therefore, only few estimates can be taken to be compared with our data. Wallén (1992) determined the phytomass of fine and coarse roots of vascular plants on elevated hummock sites in two ombrotrophic mires. One of them is located in Northern Sweden and has a permafrost layer, the other in Southern Sweden with no permafrost. Total root phytomass was shown to be practically similar in those mires (2,700–2,800 g m⁻²). Coarse roots percentage amounted to 26% in the northern mire and to 35% in the southern one. In an ombrotrophic bog in Canada the below-ground biomass was shown to range from 1,200 g m⁻² at the poor fen site to 2,400 g m⁻² at the bog hummock site (Moore et al. 2002), with coarse roots contributing from 0 to 86%, respectively. Our estimates are much lower since the manual separation of roots we employed could take into account only coarse and some fine roots, thus leading to underestimation of below-ground phytomass. The same method to estimate below-ground phytomass (stem bases, rhizomes, and roots) in southern taiga mires of Western Siberia (Vasiliev et al. 2001) gave the values of 950 g m⁻² on ridges and 1,050 g m⁻² in hollows, which are very similar to ours.

Production in mire ecosystems

In the studied ecosystems the vascular plants production varied from 15 g m⁻² year⁻¹ in the oligotrophic hollow to 136 g m⁻² year⁻¹ on the ridge and was formed mainly by dwarf shrubs in the high sites and by sedges in the low sites (Table 4). The very

low production in the oligotrophic hollow was most likely due to the nutritional limitation of production process. Somewhat higher production of vascular plants (35 g m⁻² year⁻¹) was estimated in the wet hollow of the ombrotrophic bog in Finland (Vasander 1981).

According to Backēus (1985) and Bazilevich (1993), vascular plants production ranges in boreal mires of Sweden, Finland, and Russia from 55 to 170 g m⁻² year⁻¹, displaying a trend to decrease from south to north.

In our research bryophytes production differed less among ecosystems (Table 4). The ratio of bryophytes phytomass to their production, i.e., the mean residence time of living bryophytes, ranged from 0.9 to 1.6 years, increasing in the range mesotrophic hollow—ridge—palsa—fen—oligotrophic hollow. The dominating in the oligotrophic hollow *Sphagnum linbergii* might have adapted to oligotrophic conditions and for two seasons stored nutrients in its green parts.

Bisbee et al. (2001) reviewed the estimates of bryophytes production for different climatic zones, for forests and mires of different types and by using different methods. In forests, production of bryophytes ranged from 20 to 130 g m⁻² year⁻¹. In forested mires, their production was much higher (160–330 g m⁻² year⁻¹). In Canada (Manitoba) production of bryophytes varied from 100 to 220 g m⁻² year⁻¹ along the range: bog-poor fen—intermediate fen—rich fen, with annual production of mosses reaching maximum in a poor fen (Weltzen et al. 2001). *Sphagnum fuscum* was shown to produce 130–300 g m⁻² year⁻¹ under raised bog conditions in Western Siberia (Varluigin and Liss 2001) and in a bog-poor fen complex in Canada (Waddington et al. 2003).

Grigal (1985) compared *Sphagnum* production for different latitudes (46°20′–48°50′ N) in North America and found out that in this narrow latitudinal range production did not change much, ranging 320–390 g m⁻² year⁻¹. He showed much higher production in hollows (520 g m⁻² year⁻¹) as compared hummocks on perched bogs (320 g m⁻² year⁻¹) and 370 g m⁻² year⁻¹ in hollows versus 300 g m⁻² year⁻¹ in hummocks on raised bogs. Differences between mire ecosystems of the same latitude 47°30′ N appeared to be higher than between mires of different latitudes.

Comparison of our data for southern (Vasiliev et al. 2001) and northern taiga with the data given by Grigal (1985) confirmed his conclusion about the inverse relationship between bryophyte production and latitude (Table 5).

It is necessary to mention that in northern taiga *Sphagnum* mosses reach the northern border of their area. In hollows under the influence of permafrost and low temperatures, *Sphagnum* stems and some of its capitula die off in winter. But during short summer with long daylight, the remained capitula restore continuous moss cover among *Carex* and *Eriophorum* plants. *Sphagnum* is known to reproduce vegetatively from leaves, stems, and branch fragments (Solonevich 1971). This ability of *Sphagnum* to regenerate explains its relatively high production in mires of northern taiga.

Total ANP was measured in Canada along the bog—fen—marsh gradient (Thormann and Bayley 1997). The ANP estimates appeared to be almost similar in the bog and the riverine sedge fen ($400 \text{ g m}^{-2} \text{ year}^{-1}$), decreased to $280\text{--}360 \text{ g m}^{-2} \text{ year}^{-1}$ in lacustrine and floating sedge fens, and sharply increased (to $760 \text{ g m}^{-2} \text{ year}^{-1}$) in the lacustrine marsh. The authors mentioned that along this

gradient the production of mosses and shrubs decreased, while the herb production increased. Herb and moss production exhibited bigger variation between years than among sites within 1 year. Our estimates were lower because the ecosystems we studied are located more to the north.

There is a clear lack of BNP data for mires because of the difficulties of its estimation, which was often mentioned by researchers studying the carbon cycle in mires (Wallén 1992; Saarinen 1996; Scheffer and Aerts 2000). These scarce estimates, however, prove the important role of below-ground layer in total production. In the *Carex* wetland in temperate region litter production amounted to $870 \text{ g m}^{-2} \text{ year}^{-1}$, with 25% and 75% contributed by leaves and roots, respectively (Verhoeven and Arts 1992; Aerts and De Caluwe 1994).

If we take into account not only rhizomes and coarse roots, but also fine roots, then BNP estimates for 0–25 cm layer reach $560 \text{ g m}^{-2} \text{ year}^{-1}$ (Wallén 1992). This estimate was obtained by the isotope-labelling technique. Fine root production estimated by using in-growth cores is an order of magnitude lower, reaching in the 0–39 cm layer of the ombrotrophic open bog in central Sweden only 51 g m^{-2}

Table 5 Relationship of bryophyte production to latitude

Location	Latitude, N	Species	Bryophyte production, $\text{g m}^{-2} \text{ year}^{-1}$	Source
North America	46°20'	<i>Sphagnum</i> sp.	390	Elling and Knighton (1984)
North America	47°30'	<i>Sphagnum angustifolium</i> , <i>Sphagnum magellanicum</i> <i>Sphagnum fuscum</i> , <i>Sphagnum fallax</i>	320–380	Grigal (1985)
North America	48°50'	<i>Sphagnum fuscum</i>	360	Pakarinen and Gorham (1983)
North America	48°47'	<i>Sphagnum fuscum</i> <i>Sphagnum capillifolium</i>	114–290	Waddington et al. (2003)
North America	54°28'	<i>Sphagnum</i> spp.	140–225	Moore et al. (2002)
Asia, Western Siberia	56°51'	<i>Sphagnum fuscum</i> , <i>Sphagnum angustifolium</i> , <i>Sphagnum fallax</i> , <i>Sphagnum majus</i> , <i>Sphagnum balticum</i>	270–300	Kosykh et al. (2003)
Asia, Western Siberia	60°50'	<i>Sphagnum fuscum</i> , <i>Sphagnum angustifolium</i> , <i>Sphagnum majus</i> , <i>Sphagnum balticum</i> , <i>Sphagnum lindbergii</i>	255–280	Kosykh (2003)
Asia, Western Siberia	63°17'	<i>Sphagnum fuscum</i> , <i>Sphagnum fallax</i> , <i>Sphagnum riparium</i> , <i>Sphagnum lindbergii</i>	200–280	This study

year⁻¹ on hummocks and 86 g m⁻² year⁻¹ on lawns (Backēus 1990). Thus, the BNP estimates available in literature strongly depend on the estimation methods employed and specific fractions of the below-ground phytomass taken into account.

The NPP estimates for mire ecosystems range from 650 to 1940 g m⁻² year⁻¹ (Table 6) depending on the latitude, mire type, seasonal weather and method used.

We can analyse the relationship between production process and the type of mire ecosystem and the year of studying for the northern taiga of Western Siberia. Principal components analysis of the log-transformed data, arranged in a matrix with study sites of different years as cases and production characteristics as variables, groups together different years of one and the same study site and shows clear separation of all study sites from one another (Fig. 6). Thus, yearly changes in overall production process seemed to be less pronounced than changes because of ecosystem characteristics. The first principal component, accounting for 56% of the total variance of the log-transformed original data, clearly separated the flat palsa mire (negative semiplane, with exception for the year 2000 point) from the ridge-hollow-pool mire and the fen. So we believe the first component represented the influence of discontinuous permafrost on plant production in the studied mires. The second principal component, accounting for 25% of the total variance in the log-transformed original data, separates dry sites (positive semiplane) from the wet ones (negative semiplane, with exception of oligotrophic hollow in the year 2000) (Fig. 6). The positive pole of this component is determined by production of lichens and mosses (factor loading 0.58), whereas the negative pole is determined by ANP of sedges and herbs and BNP (factor loadings –0.62 and –0.64, respectively). Thus, this component most likely represented the influence of water table depth on the structure of production process: in drier sites ANP (specifically that of lichen and mosses)

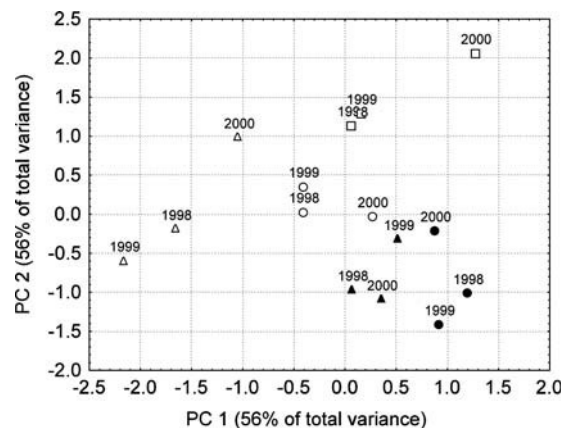


Fig. 6 Location of study sites (factor scores) according to their production in different years in the plane of principal components 1 and 2. ○—palsa, □—ridge, △—oligotrophic hollow, ▲—mesotrophic hollow, and ●—fen

appeared to play the major role, whereas in wet sites total production was governed by BNP and ANP of sedges and herbs.

Overall we hypothesize that phytomass standing crop and production in the boreal mire ecosystems are driven by different factors: depth of water table is of primarily importance for supporting standing crop, whereas more severe temperature regime associated with permafrost influence is of utmost importance for production process.

Our data and findings of other researchers were used for mapping NPP in Western Siberian wetlands (Peregon et al. 2005). It was shown that most of NPP was produced in the taiga zone and reached 320.8 Tg of dry matter a year, with the northern taiga, where we carried our research, contributing 19%.

Thus our research provides for the first time the estimates of living phytomass and NPP in northern taiga mire ecosystems of the West Siberia, specifying the contribution of below-ground plants organs and Sphagnum mosses by using new measurement technique. We hope these estimates will be used to simulate explicitly the role of Siberian peatlands

Table 6 The NPP estimates for some mire ecosystems

Location	Latitude, N	NPP, g m ⁻² year ⁻¹	Source
Canada, Southern Manitoba	49°53'	990–1940	Reader and Stewart (1972)
Russia, Western Siberia	56°51'	990–1010	Vasiliev et al. (2001)
Sweden, south	57°06'	800	Wallén (1992)
Russia, Western Siberia	63°17'	350–960	this study

both in the global carbon cycle and the CO₂ budget of Russia.

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