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CO₂ Emissions of the Non-tree Vegetation Cover in larch (*Larix gmelinii* (Rupr.) Rupr.) Stands in the Central Evenkia Region of Siberia, Russia

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Abstract

CO₂ emissions from various vegetation components were studied in larch-dominated stands (*Larix gmelinii* (Rupr.) Rupr.) in the Central Evenkia region of Siberia, Russia, during growing season in 2001. We found a clear relationship between air temperature and CO₂ emission rate of the dominant vegetation components (such as *Sphagnum* and green mosses, lichens, and dwarf shrubs). The CO₂ emission rate of *Sphagnum*, green mosses, and lichens (measured as CO₂ evolution from their surface) ranged from 0.04 to 0.24 mg CO₂ g⁻¹ oven-dry weight (odw) h⁻¹ during growing season. The CO₂ emission rate of the aboveground parts of dwarf shrubs ranged from 0.65 to 5.54 mg CO₂ g⁻¹ odw h⁻¹. The contribution of the different components of the vegetation cover varied among stand types; for example, in *Sphagnum* associations, up to 94% of the total CO₂ emission occurred from the *Sphagnum*–green mosses–lichen cover, whereas in stands dominated by dwarf shrubs, 90% of total CO₂ emission occurs from the dwarf shrubs.

Key words: CO₂ emission, Dwarf shrubs, Moss-lichen cover, Siberia, Vegetation cover

Introduction

Boreal forest ecosystems are one of the main reservoirs of terrestrial organic carbon and are being studied closely by many investigators, especially with respect to the effects of global climate change (Raich and Schlesinger 1992, Wang and Polglase 1995, Apps 2002). In this context, the vegetation cover is of particular interest since it is an important component of the forest ecosystem and plays an essential role in the dynamics and accumulation of nutrients and carbon in boreal forests growing in areas with permafrost (Fukuda 1994; Schulze *et al.* 1997, 1999). Because the carbon dynamics of boreal trees are relatively well understood (Al'tergoth and Hitrovo 1970, Landhausser *et al.* 1996, Mori *et al.* 1998), we have chosen to focus on the vegetation cover, which has not been studied for these ecosystems. The term "vegetation cover" represents both the live vegetation cover (mosses, lichens, and dwarf shrubs) and the litter layer (Melekhov 1980), but does not include the tree layer. The biomass of live vegetation and litter can be quite large in boreal forest ecosystems. Therefore, it is necessary to better understand CO₂ emissions from these vegetated surfaces. Moreover, we must evaluate the effect of various environmental factors, such as temperature and moisture, on the CO₂ emission from the vegetation cover to obtain crucial data on the CO₂ dynamics of this ecosystem component. The objective

of our study was to determine the CO₂ emission rate of individual components of the vegetation cover and their contribution to total CO₂ emissions from the surface as a function of their biomass in several types of larch stands.

Materials and Methods

1. Description of the study site

The research was carried out from June to September 2001 in fixed experimental plots (EP) established in several types of stand dominated by larch (*Larix gmelinii* (Rupr.) Rupr.) in the Central Evenkia region of Siberia, Russia (64°18'N, 100°11'E) as follows: a dwarf shrub–*Sphagnum* larch stand (EP I-1) situated in the bottom of a valley; a crowberry (*Empetrum nigrum* L.)–bearberry (*Arctostaphylos uva-ursi* L.) larch stand (EP I-2) located on terraces; a cowberry (*Vaccinium vitis-idaea* L.)–green mosses larch stand (EP I-3) in the middle of a northeast-facing slope; a cowberry–blueberry (*Vaccinium uliginosum* L.)–green mosses–lichen larch stand (EP II-2) located on the floodplain of a river; and a *Ledum* (*Ledum palustre* L.)–blueberry–lichen–green mosses larch stand (EP IV-2) in the middle of a west-facing slope.

The characteristics of each plot are given in Table 1. These plots are characterized by differences in the thickness of the vegetation cover and in productivity. Climatic and soil characteristics of the study site were

given by Abaimov *et al.* (1999) and Ershov (1998). Continuous permafrost presenting in this region controls hydrothermal conditions and other environmental factors. According to Prokushkin *et al.* (2005), at the same to ours, studied larch stands permafrost occur at the depth from 0 to 60 cm because of the active layer is deepening during growing season. During the research period from June to September, air

and soil temperatures (daily mean values, Fig. 1) were measured daily on a twenty-four hour basis with auto-logging thermometers (TR 51-A, T&D, Matsumoto, Japan). Air temperatures at breast height during the research period averaged +15.0°C, soil temperature at a depth of 10 cm averaged +7.7°C, and the amount of precipitation from June to September totaled 300 mm.

Table 1. Characteristics of the experimental plots established in the larch stands*.

EP	Composition	Mean tree diameter (cm)	Mean tree height (m)	Canopy closure (%)	Age (years)	Vegetation cover thickness, including litter (cm)	Stand density (trees ha ⁻¹)
I-1	100% L.g.**	4.0	4.2	16	72-92	20-25	2670
I-2	90% L.g. & 10% B	6.2	6.1	20	72-92	3-5	770
I-3	100% L.g.	6.6	8.2	57	73-92	8-10	2910
II-2	100% L.g.	7.8	7.4	30	149-260	8-10	2000
IV-2	100% L.g.	9.0	8.0	37	150	15-20	1830

Notes: * According to Abaimov *et al.* (1997), Prokushkin *et al.* (2002, 2006);

** L.g., *Larix gmelinii* (Rupr.) Rupr.; B, *Betula pendula* Roth.

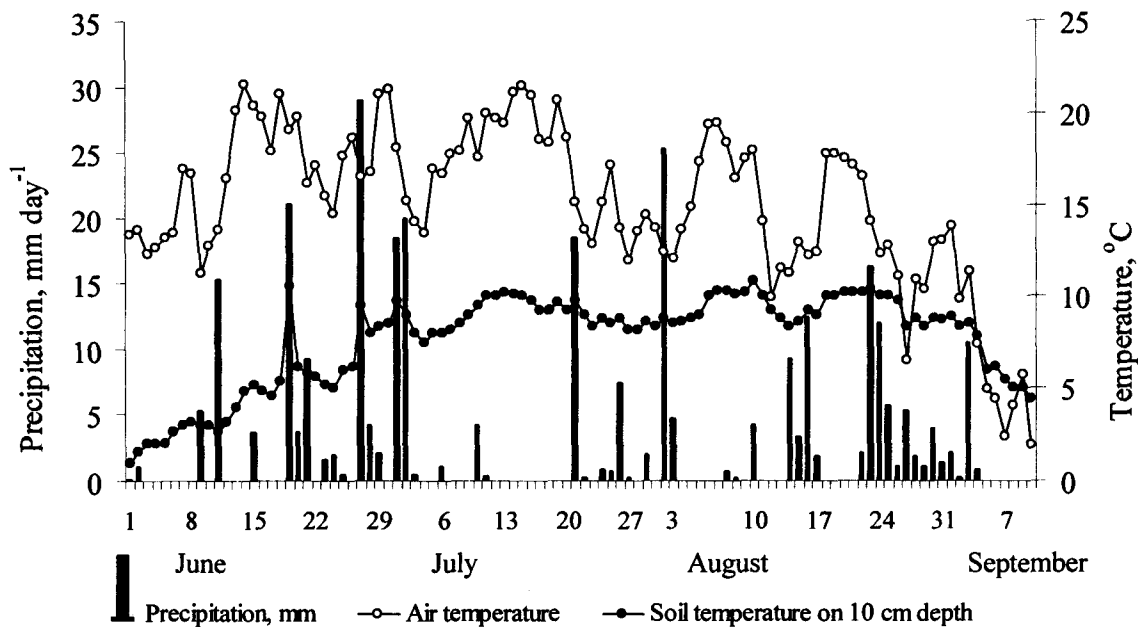


Fig. 1. Mean air and soil temperatures (calculated on the 24 hours basis) and precipitation during the study period.

2. Plant materials

We used all components of the vegetation cover, including *Sphagnum* mosses (*Sphagnum fuscum* (Schimp.) Klinggr., *Sphagnum magellanicum* Brid., *Sphagnum wulfianum* Girg.), green mosses (*Aulacomnium turgidum* (Wahlenb.) Schwaegr., *Dicranum polysetum* Sw., *Hylocomium splendens* (Hedw.) B. S. G., *Pleurozium schreberi* (Brid.) Mitt., *Ptilidium ciliare* (L.) Hampe and others), and lichens (*Cetraria islandica* (L.) Ach., *Cladina arbuscula* (Wallr.), *Cladina rangiferina* (L.) Web., *Cladina stellaris* (Opiz) Brodo, *Peltigera aphthosa* (L.) Willd. and others), including both the litter layer and the roots of dwarf shrubs, and the aboveground parts of the dwarf shrubs (*Vaccinium vitis-idaea*, *Vaccinium uliginosum*, *Ledum palustre*, *Empetrum nigrum*, *Arctostaphylos uva-ursi*) for the CO₂ emission measurements. These were the dominant plants in the studied stands based on projected cover and biomass. We did not differentiate between different communities of *Sphagnum*, green mosses, and lichens based on their species composition.

Using method of Ponyatovskaya (1964) for biomass assessment, each of the component biomass was determined for use in the calculation of the CO₂ emissions using 20 × 25 cm plots equal in depth to the depth of the living vegetation with 7 to 10 replications in each stand type, but not in the same place of CO₂ emissions measurement, it was separated by a significant distance (about 10 m) and the experimental plot size for each stand was 20 × 20 m in each stand type, so it could not affect environmental conditions. To estimate biomass, we destructively sampled all the vegetation inside each 20 × 25 cm plot (*Sphagnum*, green mosses, and lichens, plus the litter and dwarf shrub roots to the permafrost level, and the aboveground parts of dwarf shrubs) and sorted it by *Sphagnum*, green moss, lichen and dwarf shrub groups. We oven-dried all plant materials to obtain the

oven-dried weight (odw) at 104°C and calculated the total stocks (t ha⁻¹) in each plot. Information about the composition, projected area, and biomass of each component of the vegetation cover is given in Table 2.

3. CO₂ emission measurements

We measured CO₂ emission rates of the non-shrub components of the vegetation cover *in situ* using an infrared gas analyzer (IRGA; Li-6200, LiCor, Lincoln, NE, USA) equipped with a soil (dark) respiration chamber (model 6000-09), which excludes the effects of CO₂ assimilation by plants inside the chamber. The chamber volume was 962 cm³, and it covered a soil surface area of 78.5 cm². The flow rate was set to between 0.1 and 2 L min⁻¹, with the rate adjusted manually to produce steady-state conditions within the chamber. The respiration chambers were inserted to a depth of 10 cm in the soil in plots with *Sphagnum*–green mosses–lichen cover, thus the measurements also included CO₂ emissions of litter, any root, and soil in these samples. When we measured respiration by dwarf shrubs, we used specially designed plastic rings inserted to a depth of 10 cm in the soil. The height of the plastic rings (from 10 to 25 cm) were changed according to the height of the dwarf shrubs and the chamber volume for the calculation of the CO₂ emission rate was changed according to the height of the rings. In addition, we isolated the aboveground parts of the shrubs in the chamber from the underlying *Sphagnum*, green mosses, and lichen using clay and plastic film insulating materials to exclude CO₂ flux through the ground surface; thus, we only recorded respiration rates for the aboveground parts of the dwarf shrubs. The measurement of root respiration of dwarf shrubs was included in measurements of mosses and lichens associated with litter and any roots.

We studied the relationship between temperature and CO₂ emissions for every component of the vegetation cover from June to September by controlling the air

Table 2. Projected cover (%) and biomass (t ha⁻¹) of the vegetation cover in the studied larch stands.

EP	<i>Sphagnum</i> with litter and roots	Green mosses with litter and roots	Lichens with litter and roots	Dwarf shrubs (aboveground parts)***	Total biomass
I-1	20* 81.39**	26 4.48	32 8.08	27 0.69	94.64
I-2	-	-	8 9.12	33 3.6	12.72
I-3	-	55 57.72	6 10.95	14 2.07	70.74
II-2	-	47 19.99	34 14.48	17 2.12	36.59
IV-2	-	85 39.42	30 25.84	52 0.81	66.07

Notes: EP experimental plot.

* Projected cover (%). ** Biomass (t ha⁻¹).

*** Sum for all dwarf shrubs. – not observed in the plot.

temperature inside the chamber and recording CO₂ emission at temperatures from +5 to +40°C at 5°C intervals. Air temperatures inside the chamber were checked using the display of the IRGA to within 0.5°C. To cool the air inside the chamber, we used ice packs; to heat the air, we used hot water containers. The air temperature inside the respiration chamber was obtained using the thermometer mounted inside the chamber. Before every CO₂ emission measurement at each temperature, we left the chamber for about 40 min until its temperature had stabilized. CO₂ emission rates for the vegetation cover components were calculated on the basis of oven-dry weight. For that, we performed destructive sampling of *Sphagnum* moss, green mosses, lichens and dwarf shrubs after each measurement. Then, we removed mineral soil and separated the measured materials into live and dead parts (including litter and roots), then oven-dried the materials at 104°C to obtain the oven-dried weights (odw). In this connection, we created new CO₂ emission measurement plots after each measurement of CO₂ emissions and destructive sampling of the biomass.

In the Central Evenkia region, the water content of the components of the dominant vegetation cover, excluding dwarf shrubs, ranged from 35% to 96% in different stands, varied in a narrow range for a given experimental plot (stand type) during the measurement period, and had no significant effect on the measured CO₂ emissions. Therefore, in the remainder of our analysis, we only accounted for temperature effects on the respiration rate when we calculated CO₂ emissions from the surface of the vegetation cover.

4. Calculation of temperature coefficient values and CO₂ emissions

Temperature coefficient (Q_{10}) values are typically calculated using the following equation:

$$Q_{10} = \frac{R^{T+10^{\circ}\text{C}}}{R^T} \quad [1],$$

where Q_{10} is the temperature coefficient for the CO₂ emission rate; R^T is the CO₂ emission rate (mg CO₂ g⁻¹ odw h⁻¹) at a given temperature T (°C); and $R^{T+10^{\circ}\text{C}}$ is the CO₂ emission rate at a temperature 10°C greater than T . In this study, we set T equal to the daily mean air temperature, following the method of Semikhatova (1995) that says that in the context of Adaptation Theory, it is more correct to compare plant characteristics of different habitats at typical environmental conditions.

The amount of CO₂ emitted by each component of the vegetation cover (*Sphagnum* with litter and roots; green mosses with litter and roots; lichens with litter and roots; aboveground parts of dwarf shrubs) was calculated per unit of biomass (B^{comp}) using equation [2]:

$$F^{comp} = \sum R^{comp}_{day} \times B^{comp} \times 24 \times 10^{-6} \quad [2],$$

where F^{comp} is the daily total rate of CO₂ emission (kg ha⁻¹ day⁻¹); R^{comp}_{day} is the daily mean CO₂ emission rate of each component of the vegetation cover (mg CO₂ g⁻¹

odw h⁻¹); B^{comp} is the biomass of live *Sphagnum*, green mosses, and lichen, including litter and roots or of the aboveground part of dwarf shrubs (g ha⁻¹); 24 is the number of hours in a day; and 10⁻⁶ is the conversion factor between mg and kg of CO₂.

We used STATISTICA v.6.0 (StatSoft, Tulsa, USA) for all statistical analyses.

Results and Discussion

1. Relationships between temperature and CO₂ emission rate

In boreal forests, temperature is typically the main factor that limits biological processes, including ecosystem respiration; thus, respiration rate depends most closely on temperature (Amthor 1994). Our results confirmed that vegetation moisture content had no effect on CO₂ emission, and thus, that temperature was the dominant factor. During the vegetative period, increasing temperature from +5°C to +35°C increased CO₂ emissions by *Sphagnum*, green mosses, lichens, and dwarf shrubs from 0.02 to 0.49, 0.02 to 0.60, 0.02 to 0.37, and 0.14 to 12.58 mg CO₂ g⁻¹ odw h⁻¹, respectively (Fig. 2). The temperature response of CO₂ emission followed the equations shown in Table 3. Aboveground respiration by *V. vitis-idaea* increased from 0.18 to 5.55 in June, from 1.22 to 12.58 in July, from 0.53 to 3.86 in August, from 2.56 to 7.15 mg CO₂ g⁻¹ odw h⁻¹ in September as temperatures increased from +5°C to +35°C (Fig.2). A narrower range of variation in this species in Alaskan tundra was reported by Limbach *et al.* (1982); as temperatures increased from +5°C to +30°C, CO₂ emission rate increased from 0.63 to 0.97 mg CO₂ g⁻¹ odw h⁻¹.

The CO₂ emission rate of all vegetation components increased exponentially as air temperature increased. However, in some cases the respiration rate of dwarf shrubs was higher at +5°C than at +10°C. The same phenomenon has been reported in previous studies, most of which associated this effect with the changes in the physical properties of water in plant tissues at temperatures between -3 and +5°C (Al'tergoth and Hitrovo 1970, Miroslavov 1994, Landhausser *et al.* 1996).

During the vegetative period, we observed two significant maxima for the CO₂ emission rate of dwarf shrubs: one in July and another in the first ten days of September (Fig. 3, Table 4). The results of previous studies (Evdokimova 1985, Luk'yanova *et al.* 1986, Shuvalova 1988) suggest that the July maximum occurs during the active period of development of generative organs (i.e., the bud-formation phase) and of flowering, and the second occurs during preparation for the plant's quiescent period or in response to stress imposed by early frosts. The latter hypothesis is reasonable because temperatures in the Central Evenkia region usually reached 0°C by late August. At the end of the vegetative period, when the daily mean air temperature was near 0°C and night frosts occurred, the CO₂ emission rates of *Sphagnum*, green mosses, and lichens all increased (Fig. 2). This may have resulted from the fact that soil temperature became higher than air temperature during September due to thermal lag of a

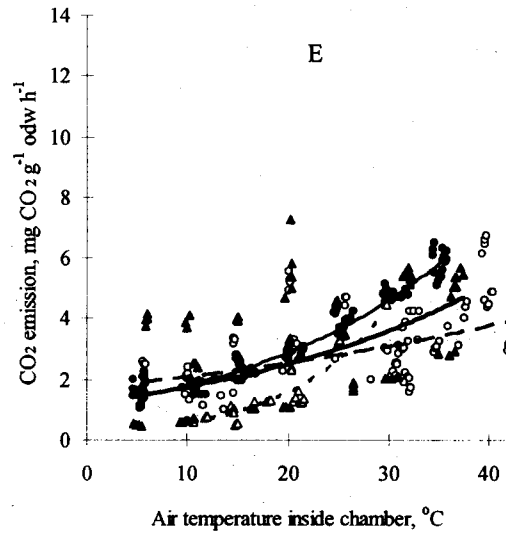
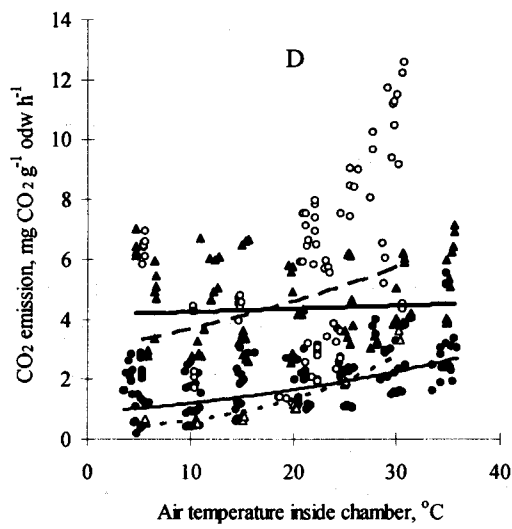
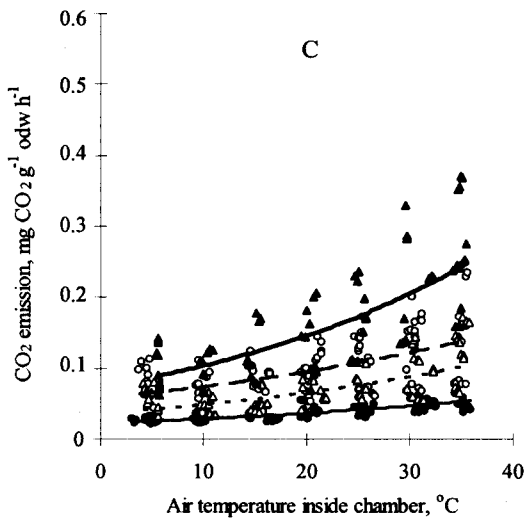
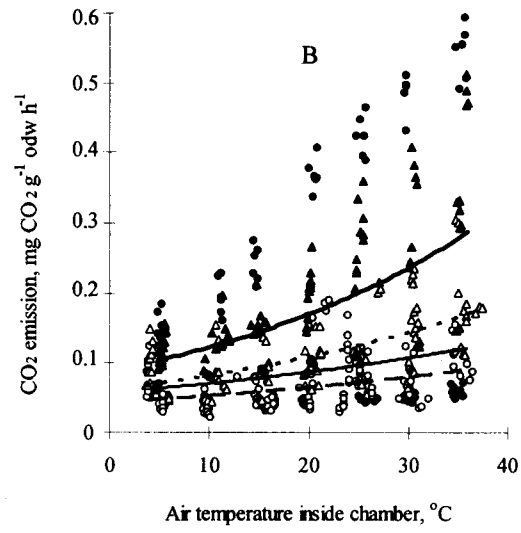
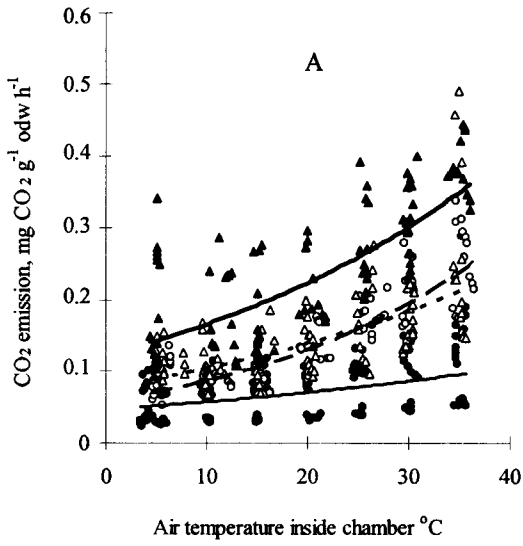
soil (Fig. 1). When the soil temperature was higher than the air temperature, thermal inversion can accelerate CO₂ diffusion in the air-filled pores in the vegetation surface and thus cause large CO₂ emissions from the *Sphagnum*–green mosses–lichen cover (Ivannikova and

Semenova 1988, Gryaz'kin and Tarasov 1989). In other words, environmental conditions at the end of growing period became more favorable for CO₂ emission into the atmosphere.

Table 3. Equations* describing the relationship between air temperature and CO₂ emission for the vegetation components of the larch stands in the study.

Vegetation component	Month	a	b	r ²	p
<i>Sphagnum</i> with litter and roots	June	0.0468	0.0206	0.22	0.000
	July	0.0581	0.0404	0.74	0.000
	August	0.0788	0.0284	0.4	0.000
	September	0.1238	0.0297	0.53	0.000
Green mosses with litter and roots	June	0.0574	0.0211	0.09	0.001
	July	0.0433	0.0206	0.1	0.000
	August	0.0619	0.0283	0.4	0.000
	September	0.0881	0.033	0.45	0.000
Lichens with litter and roots	June	0.0222	0.0247	0.58	0.000
	July	0.0575	0.025	0.37	0.000
	August	0.0361	0.0297	0.46	0.000
	September	0.0735	0.0342	0.56	0.000
<i>V. vitis-idaea</i> (aboveground parts)	June	0.8784	0.0314	0.25	0.000
	July	2.9475	0.0222	0.12	0.001
	August	0.2946	0.0749	0.77	0.000
	September	4.137	0.0025	0.003	0.651
<i>V. uliginosum</i> (aboveground parts)	June	1.1192	0.0472	0.92	0.000
	July	1.7078	0.0198	0.21	0.000
	August	0.1965	0.1035	0.79	0.000
	September	1.2114	0.0363	0.26	0.000
<i>L. palustre</i> (aboveground parts)	June	0.4657	0.044	0.58	0.000
	July	1.6942	0.019	0.06	0.002
	August	0.4942	0.0471	0.46	0.000
	September	1.5388	0.024	0.19	0.000
<i>E. nigrum</i> (aboveground parts)	June	0.1554	0.0598	0.72	0.000
	July	0.4944	0.0398	0.4	0.000
	August	0.5897	0.0295	0.34	0.000
	September	1.4584	0.015	0.23	0.000
<i>A. uva-ursi</i> (aboveground parts)	June	0.6903	0.0279	0.69	0.000
	July	0.2777	0.0464	0.32	0.000
	August	0.8796	0.0068	0.002	0.680
	September	1.9766	0.0155	0.24	0.000

Notes: * Equation has a form $R_{day}^{comp} = a e^{bT}$. In the equations, R_{day}^{comp} is the daily mean CO₂ emission rate of the vegetation component (mg CO₂ g⁻¹ odw h⁻¹) and T is the mean daily air temperature (°C).



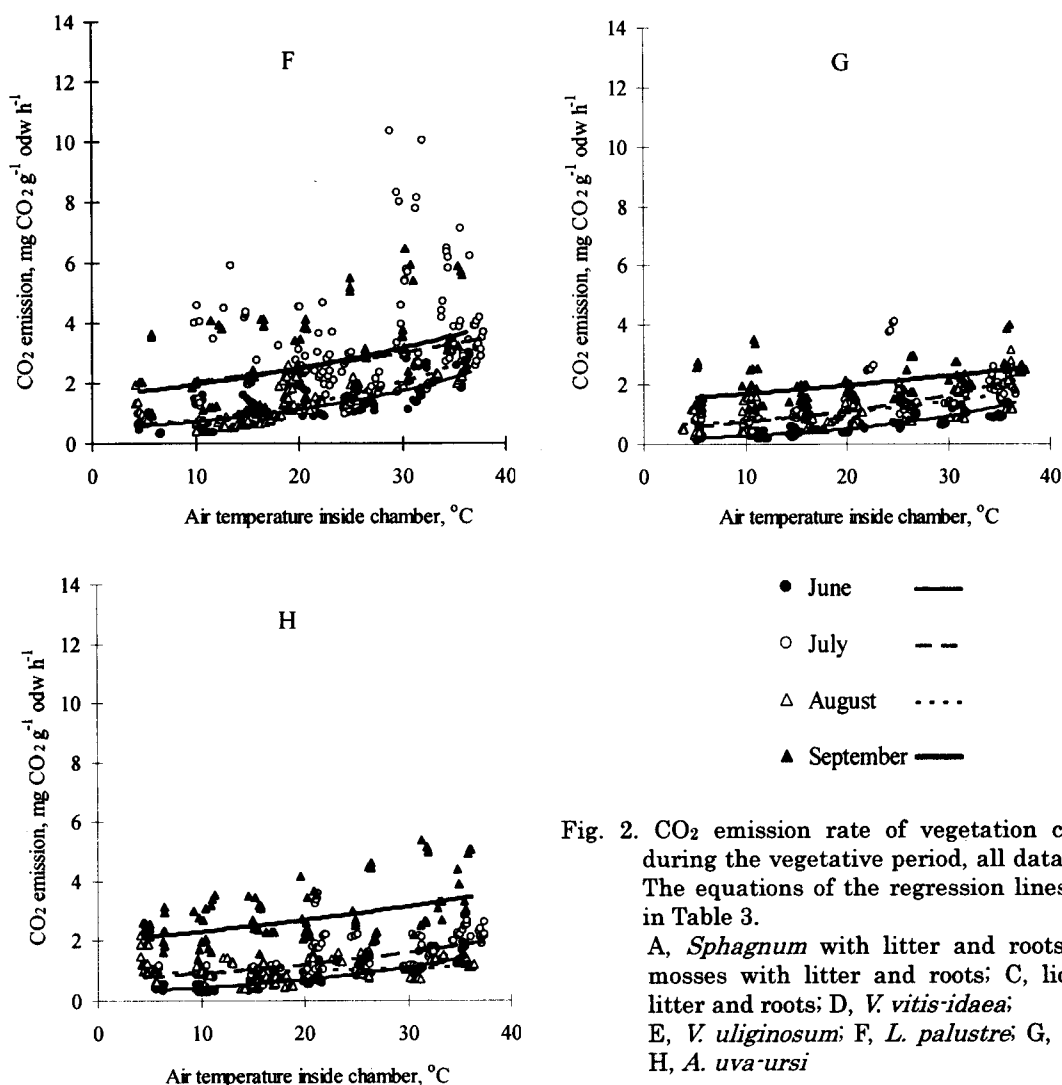


Fig. 2. CO₂ emission rate of vegetation components during the vegetative period, all data combined. The equations of the regression lines are given in Table 3.

A, *Sphagnum* with litter and roots; B, green mosses with litter and roots; C, lichens with litter and roots; D, *V. vitis-idaea*; E, *V. uliginosum*; F, *L. palustre*; G, *E. nigrum*; H, *A. uva-ursi*

Table 4. Mean values of CO₂ emission rate (mg CO₂ g⁻¹ odw h⁻¹*) of vegetation cover components during the vegetative period.

Vegetation cover component	June	July	August	September
Green mosses with roots and litter	0.146±0.014	0.074±0.004	0.123±0.006	0.189±0.011
<i>Sphagnum</i> with roots and litter	0.078±0.003	0.149±0.007	0.155±0.008	0.241±0.010
Lichens with roots and litter	0.037±0.001	0.105±0.005	0.074±0.004	0.164±0.009
Aboveground dwarf shrubs	1.61±0.05	2.81±0.09	1.25±0.03	3.08±0.07
<i>L. palustre</i>	1.37±0.06	3.19±0.14	1.33±0.06	2.86±0.16
<i>V. vitis-idaea</i>	1.88±0.08	5.54±0.32	1.43±0.26	4.56±0.15
<i>V. uliginosum</i>	3.17±0.13	3.19±0.14	1.52±0.16	3.10±0.20
<i>A. uva-ursi</i>	0.85±0.04	1.45±0.06	1.10±0.04	2.84±0.10
<i>E. nigrum</i>	0.65±0.04	1.40±0.07	1.20±0.06	2.06±0.07

Notes: * The monthly average CO₂ emission rate was calculated from the air temperature and the temperature-CO₂ emission rate relationships (Table 3)

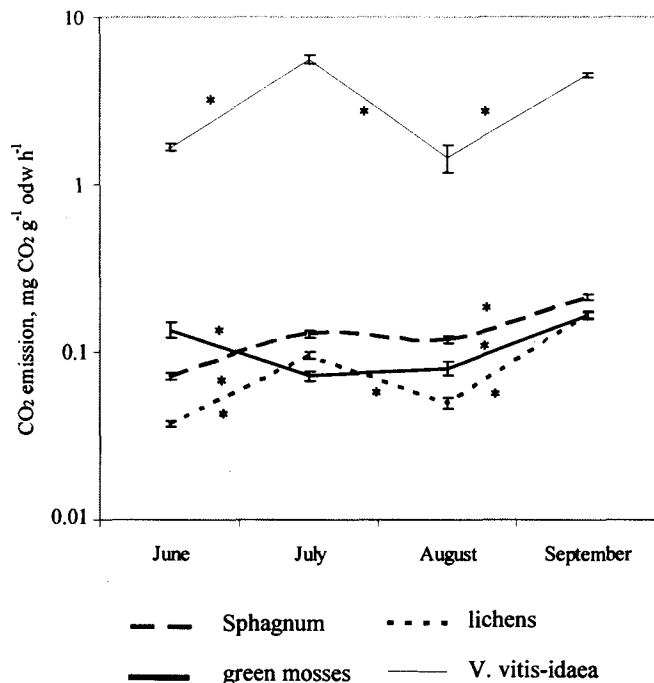


Fig. 3. Monthly mean CO₂ emission of vegetation in growing season * indicate significant change in emission rate at $p < 0.05$ (Tukey HSD test, $MS = 0.0029$, $df = 294$).

Table 5. Q_{10} of vegetation cover components during the vegetative period.

Vegetation cover component	Air temperature range	June	July	August	September
Green mosses with roots and litter	5-15°C	1.25	0.96	1.04	1.23
	15-25°C	1.61	1.41	1.41	1.60
	25-35°C	1.28	1.29	1.50	1.45
<i>Sphagnum</i> with roots and litter	5-15°C	1.10	1.13	0.94	0.92
	15-25°C	1.24	1.88	1.53	1.68
	25-35°C	1.42	1.47	1.61	1.37
Lichens with roots and litter	5-15°C	1.13	0.99	1.03	1.12
	15-25°C	1.49	1.52	1.49	1.45
	25-35°C	1.24	1.31	1.45	1.55
<i>L. palustre</i> *	5-15°C	1.46	-	0.91	1.14
	15-25°C	1.39	0.63	1.90	1.40
	25-35°C	1.88	1.98	1.07	1.07
<i>V. vitis-idaea</i> *	5-15°C	1.02	0.70	1.19	0.84
	15-25°C	1.42	1.36	2.66	0.99
	25-35°C	1.40	-	-	1.31
<i>V. uliginosum</i> *	5-15°C	1.50	0.93	-	1.15
	15-25°C	1.71	1.58	3.42	1.21
	25-35°C	1.49	0.99	-	1.52
<i>A. uva-ursi</i> *	5-15°C	1.20	0.85	0.54	1.13
	15-25°C	1.92	1.52	1.62	1.04
	25-35°C	1.52	1.56	1.05	1.42
<i>E. nigrum</i> *	5-15°C	1.67	1.35	1.00	0.95
	15-25°C	1.85	2.04	1.57	1.28
	25-35°C	1.81	1.07	1.49	1.43

Notes: * Only includes data for EP I-1, EP I-2, and EP I-3.
- insufficient temperature data.

Temperature responses of respiration (or CO₂ emission) can be evaluated using the Q_{10} temperature coefficient, which represents the increase in respiration rate for a 10°C increase in temperature. Q_{10} values for CO₂ emission of *Sphagnum*, green mosses, lichens, and dwarf shrubs ranged from 0.92 to 1.88, 0.96 to 1.61, 0.99 to 1.55, and 0.54 to 3.42, respectively, during the vegetative period (the average values presented are the minimum and maximum for all months combined, Table 5). The fact that Q_{10} was < 1.88 for *Sphagnum*, green mosses, and lichens (Table 5) indicates a dominant effect of temperature on physical processes (e.g., diffusion of CO₂) rather than biological processes (root and microbial respiration) during the vegetative period (Semikhatova 1968). In contrast, the higher Q_{10} values of dwarf shrubs (up to 3.42) during growing period were caused by biological processes (plant respiration) depending on temperature (Table 5). Some studies have reported very high values (3.0) for Q_{10} of plants at low air temperatures (+5 to +10°C), but only for species that are not psychrotolerant during the period of adaptation to low temperatures (Yokota and Hagihara 1996). Under the permafrost conditions of the Central Evenkia region (Table 5), we have not observed such a large increase of Q_{10} in dwarf shrubs that can adapt to northern areas at low temperatures (+5 to +15°C). We found that the average (June to September) Q_{10} value for the deciduous dwarf shrub *V. uliginosum* (= 1.55, maximum $Q_{10} = 3.42$) was greater than that of evergreen dwarf shrubs (*V. vitis-idaea*, *L. palustre*, *E. nigrum*, *A. uva-ursi*), which ranged from 1.29 to 1.38 (Table 5). In other words, deciduous dwarf shrubs are more sensitive to temperature changes than evergreen ones and incur supplemental energy costs to permit normal functioning under the severe taiga conditions in the Central Evenkia region (Limbach et al. 1982). Overall, respiration rate of the aboveground parts of the dwarf shrubs was ten times that of the *Sphagnum*, green mosses, and lichens, including litter and roots.

2. CO₂ emission by the vegetation cover in larch-dominated stands

Our studies showed that the CO₂ emission rate of green mosses (with litter and roots) differed little from that of *Sphagnum* (with litter and roots): 0.074 to 0.189 mg CO₂ g⁻¹ odw h⁻¹ versus 0.078 to 0.241 mg CO₂ g⁻¹ odw h⁻¹, respectively (Table 4). The total daily CO₂ emission (Table 6) from each component of the vegetation cover in each larch stand was calculated using equation [2] on the basis of the relationships between air temperature and CO₂ emission (Table 3) for each month and the biomass of each component in each stand type (Table 2). The total CO₂ emission rate was calculated using the daily mean air temperature. For the green mosses (with litter and roots), CO₂ emissions during the vegetative period averaged from 6.59 to 152.86 kg ha⁻¹ day⁻¹ (Table 6), depending on the stand type. For the *Sphagnum* (with litter and roots) in dwarf shrub-*Sphagnum* larch stands (EP I-1), CO₂ emissions during the vegetative period averaged from 129.29 to 295.94 kg ha⁻¹ day⁻¹ (Table 6). Thus, despite their low CO₂ emission rate, the large stocks of green

mosses and *Sphagnum* make these vegetation components important sources of atmospheric CO₂, like in EP I-1. Their contribution to the CO₂ emission amounts to 2% to 86% of the total emission by the vegetation cover, depending on the type of larch stand (Fig. 4).

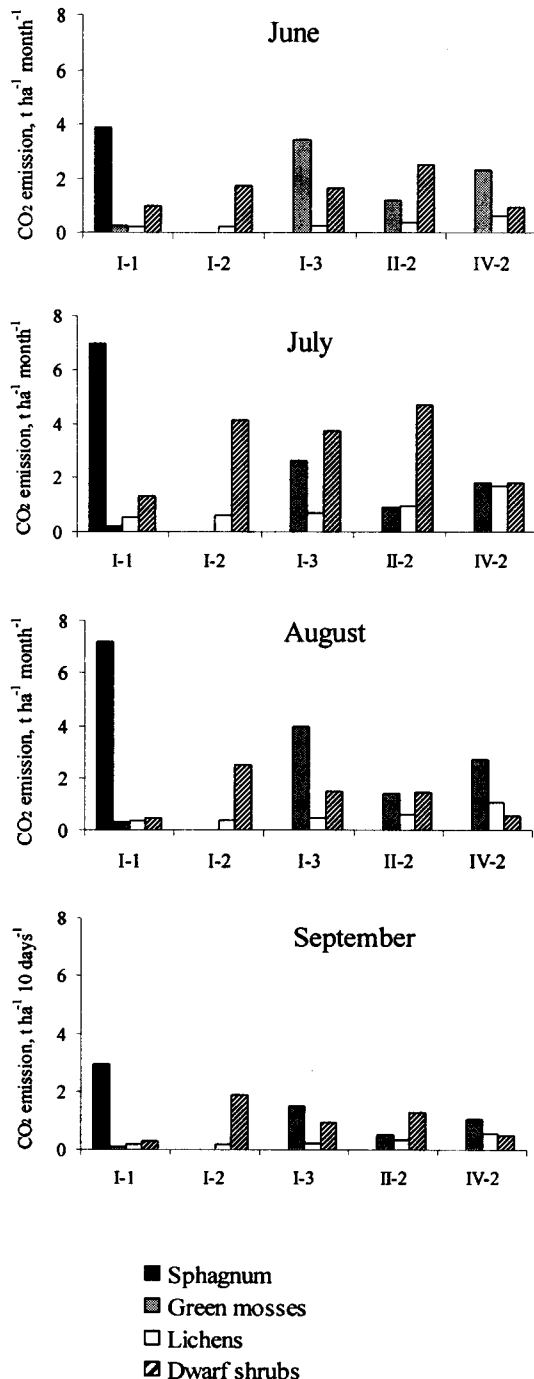


Fig. 4. CO₂ emission by *Sphagnum*, green mosses, lichens, and dwarf shrubs in the studied larch stands during the 2001 vegetative period. For the first three vegetation components, CO₂ emission includes that of the litter and roots underlying this vegetation; for the dwarf shrubs, only the aboveground components are included.

Our findings for Central Evenkia are supported by previously published data. For example, Inoue *et al.* (1995) evaluated CO₂ emission by the vegetation cover in peat wetlands in western Siberia and reported a rate of 108.8 mg C m⁻² h⁻¹ (equivalent to 96.6 kg CO₂ ha⁻¹ day⁻¹). Blodau and Moore (2003) estimated CO₂ emissions in Canadian peat wetlands to be between 6.1 and 140 mmol CO₂ m⁻² day⁻¹ (equivalent to 2.7 to 62.0 kg ha⁻¹ day⁻¹), and Bubier *et al.* (2003) reported values of 2.1 to 6.1 μmol CO₂ m⁻² sec⁻¹ (equivalent to 79.8 to 231.9 kg ha⁻¹ day⁻¹) for peat wetlands near Lake Ontario. Silvola *et al.* (1996) studied CO₂ emissions by tundra (Finland) and reported values of about 60 to 200 g C m⁻² per year (equivalent to 6.1 to 20.3 kg CO₂ ha⁻¹ day⁻¹).

The CO₂ emission rate of lichens (with litter and roots) averaged from 0.037 to 0.164 mg CO₂ g⁻¹ odw h⁻¹ (Table 4). This is close to previously reported respiration rates for lichens; for example, Nash (1996) reported values of from 0 to 5 mg CO₂ g⁻¹ odw h⁻¹ (Arctic). Based on the biomass of lichens with roots and litter (Table 2), total daily CO₂ emissions during the vegetative period averaged from 6.53 to 57.58 kg ha⁻¹ day⁻¹ (Table 6); that is, their contribution to total CO₂ emission by the vegetation cover amounted to 4% to 32%, depending on the stand type (Fig. 4). On the whole, CO₂ emission by the *Sphagnum*, green mosses, and lichen components of the vegetation cover amounted to between 10% and 94% of the total CO₂ emissions, including dwarf shrubs (Fig. 4).

The CO₂ emission rate of the dwarf shrubs (aboveground parts) averaged from 0.65 to 5.54 mg CO₂ g⁻¹ odw h⁻¹ during the vegetative period (Table 4). Larher (1981) found similar respiration rates by dwarf shrubs (from 0.2 to 16.5 mg CO₂ g⁻¹ odw h⁻¹) in mountain areas of the Tyrolean Alps, and Gerasimenko *et al.* (1996) reported a mean value of ca. 5.6 mg CO₂ g⁻¹ odw h⁻¹ for dwarf shrubs on Russia's Vrangel Island. Based on their biomass in the larch stands (Table 2), total daily CO₂ emission from the aboveground parts of the dwarf shrubs during the vegetative period ranged from 0.22 to 99.70 kg ha⁻¹ day⁻¹ (Table 6), depending on the stand type. The CO₂ emission rate of the dwarf shrubs thus seems to be an important component of total CO₂ evolution by the vegetation cover (for example, in EP I-2), and amounts to 6% to 90% of the total (Fig. 3) depending on the stand type. The maximum contribution was by *L. palustre* and the minimum was by *E. nigrum* and *V. uliginosum*.

CO₂ emission by the vegetation cover reached its maximum in July (Fig. 4), during the period of active growth with favorable weather, and this increase is likely to be related to rising metabolic costs for growth and development of plant tissues at that time. Among the studied larch stands, the dwarf shrub-*Sphagnum* larch stand (EP I-1) produced the maximum CO₂ emission from the vegetation cover (Fig. 4). This results from the dominance and large biomass of *Sphagnum* in this stand type (Table 2). Despite the low CO₂ emission rate of *Sphagnum* (Fig. 2A), the large biomass made this genus responsible for a large amount of CO₂ emitted from the surface in this stand (Fig. 4).

Table 6. Total daily emission of CO₂ by the vegetation components (kg ha⁻¹ day⁻¹*) in the studied larch stands during 4 months of the vegetative season in 2001.

Vegetation cover component	June	July	August	September
Green mosses with roots and litter	from 8.80±0.10 to 113.42±1.33	from 6.59±0.07 to 84.90±0.89	from 10.01±0.16 to 128.92±2.07	from 11.87±0.48 to 152.86±6.17
<i>Sphagnum</i> with roots and litter	129.29±1.48	225.04±4.63	231.75±3.74	295.94±10.72
Lichens with roots and litter	from 6.53±0.09 to 20.87±0.29	from 17.01±0.22 to 54.38±0.69	from 10.74±0.18 to 34.35±0.58	from 18.00±0.75 to 57.58±2.41
Aboveground parts of dwarf shrubs	from 32.17±0.75 to 84.20±1.95	from 42.02±0.43 to 152.73±1.62	from 15.28±0.74 to 80.27±1.26	from 30.59±1.00 to 188.03±2.84
<i>L. palustre</i> **	from 4.00±0.10 to 41.92±1.02	from 9.52±0.09 to 99.70±0.97	from 3.99±0.11 to 41.80±1.11	from 7.38±0.21 to 77.31±2.25
<i>V. vitis-idaea</i> **	from 2.15±0.04 to 16.83±0.29	from 6.17±0.07 to 48.35±0.55	from 1.27±0.05 to 9.95±0.42	from 6.07±0.02 to 47.44±0.14
<i>V. uliginosum</i> **	from 0.60±0.02 to 27.50±0.72	from 0.57±0.01 to 26.33±0.27	from 0.22±0.01 to 10.01±0.58	from 0.37±0.02 to 17.15±0.76
<i>A. uva-ursi</i> **	19.31±0.50	35.04±0.50	30.71±0.12	69.47±1.29
<i>E. nigrum</i> **	from 0.41±0.01 to 16.19±0.54	from 0.93±0.02 to 36.56±0.74	from 0.87±0.01 to 33.99±0.57	from 1.55±0.03 to 60.76±1.09

Notes: * Emission rate was calculated based on the biomass in Table 2;

** Only includes data for EP I-1, EP I-2, and EP I-3.

In this stand type, CO₂ emission from the remaining vegetation cover components was less than 30% of the total emission.

Our results suggest that dwarf shrubs (aboveground parts) and mosses (with litter and roots) are both important components of total CO₂ emission by the vegetation cover, especially in July, when they grow most actively. Dwarf shrub biomass in stand types EP I-1, EP I-2, EP I-3, EP II-1, and EP IV-2 amounted to 0.7%, 28%, 2.9%, 5.8%, and 1.2% of the total vegetation cover biomass, respectively. However, CO₂ emission by dwarf shrubs per unit area was higher than that of lichens (with litter and roots) in all plots except EP IV-2 during the vegetative period.

The proportion of total CO₂ emission by mosses and lichens (with litter and roots) varied little during the vegetative period. This probably resulted from the stable weather during the study period (Fig. 1). Precipitation occurred throughout the vegetative period (June, 99 mm; July, 99 mm; August, 87 mm; and the first 10 days of September, 15 mm) and did not appear to affect the physical properties of the vegetation cover and litter and did not influence CO₂ emission by the vegetation cover. Similarly, there was little influence of air temperature on the vegetation cover components during the vegetative period. Average monthly air temperature remained stable during the growing period

(June, +16.7°C; July, +16.8°C; August, +14.3°C), though the first 10 days of September were noticeably cooler (+6.6°C). Because of these factors, the proportion of total CO₂ emission accounted for by *Sphagnum*, green mosses, and lichens (with roots and litter) was also stable during the vegetative period, especially in larch stands with high biomass in the vegetation cover (e.g., EP I-1, EP I-3, and EP IV-2). The contribution of these vegetation components to total CO₂ emission in these stand types ranged up to 20%, depending on the temperature. Only in July did this contribution decrease, and this seems to have resulted from increased respiration by dwarf shrubs (Fig. 4).

Conclusions

In this study, we determined the relationship between temperature and CO₂ emission by dwarf shrubs, *Sphagnum*, green mosses, and lichen cover during the vegetative period, and we assessed seasonal CO₂ emission from the vegetation cover based on these relationships. Seasonal changes in CO₂ emission rate of *Sphagnum*, green mosses, and lichens (with litter and roots) were not clearly defined, whereas dwarf shrubs showed obvious seasonal changes. We observed two significant peaks in the respiration rate of dwarf shrubs: one in July and another in September, with a minimum

in August. Total daily CO₂ production by the vegetation cover in larch stands varied among seasons and stand types. The contribution of dwarf shrubs to CO₂ emission increased in the middle of the summer (July), probably as a result of increased respiration costs for growth and metabolism. Correspondingly, the contribution of CO₂ emission by *Sphagnum*, green mosses, and lichens decreased at that time. Among the dwarf shrubs, *L. palustre* had the largest contribution to total CO₂ emission, and the minimum contribution was by *E. nigrum* and *V. uliginosum*. The overall contribution of dwarf shrub CO₂ emission to CO₂ emission by the vegetation cover ranged from 6% to 90%, depending on the stand type. CO₂ emission by the mosses and lichens accounted for a considerable part of total CO₂ emission by the vegetation cover, especially in *Sphagnum* associations, and varied between 10% and 94%, depending on the stand type. This contribution related to the considerable biomass in the live components of the vegetation cover and in the underlying roots and litter.

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References

- Abaimov, A.P., Bondarev, A.I., Zyryanova, O.A. and Shitova, S.A. (1997) Polar forests of Krasnoyarsk region. Novosibirsk, Nauka, Siberian Enterprise, Russian Academy of Sciences, pp. 208 (in Russian with English summary).
- Abaimov, A.P., Prokushkin, S.G., Matsuura, Y., Osawa, A., Takenaka A. and Kajimoto, T. (1999) Wildfire and cutting effects on larch ecosystem permafrost dynamics in Central Siberia. *In: Shibuya, M., Takahashi, K. and Inoue, G. (eds.) Proc. of the 7th Symposium on the joint Siberian permafrost studies between Japan and Russia in 1998.* National Institute of Environmental Sciences, Tsukuba, Japan, 48-58.
- Al'tergoth, V.F. and Hitrovo, E.V. (1970) Respiratory metabolism as an index of seasonal metabolic activity of wood plants in Eastern Siberia. *Russian J. Plant Physiol.*, 17: 1156-1163 (in Russian with English summary).
- Amthor, J.S. (1994) Plant respiratory responses to the environment and their effects on the carbon balance. *In: Wilkinson, R.E. (ed.) Plant-environmental interactions.* Marcel Dekker, New York, 501-554.
- Apps, M.J. (2002) Carbon budget of the boreal forests of the American continent. *In: Mikhina, E.I. and Muratova, E.N. (eds.) Abstracts of XI International Conference IBFRA and Workshop GOF C "Boreal Forests and Environment: Local, Regional and Global Scales", V. N. Sukachev Institute of Forest Siberian Branch of Russian Academy of Sciences, Krasnoyarsk, Russia, 8.*
- Blodau, C. and Moore, T.R. (2003) Experimental response of peatland carbon dynamics to a water table fluctuation. *Aquatic Sci.*, 65: 47-62.
- Bubier, J.L., Bhatia, G., Moore, T.R., Roulet, N.T. and Lafleur, P.M. (2003) Spatial and temporal variability in growing-season net ecosystem carbon dioxide exchange at a large peatland in Ontario, Canada. *Ecosystems*, 6: 353-367.
- Ershov, Y.I. (1998) Soil-geographic zoning of Krasnoyarsk region. *Geography and Nat. Resour.*, 2: 110-118 (in Russian).
- Evdokimova, R.M. (1985) Growth and respiration rate of *Oxycoccus palustris* (Ericaceae) shoots. *Bot. J.*, 70: 1237-1240 (in Russian with English summary).
- Fukuda, M. (1994) Occurrence of ice-complex (Edoma) in Lena river delta region and big Lhyavosky Island, high Arctic Eastern Siberia. *In: Inoue, G. (ed.) Proc. of the 2nd Symposium on the Joint Siberian Permafrost Studies between Japan and Russia in 1993,* Isebu, Tsukuba, Japan, 5-13.
- Gerasimenko, T.V., Kaeybeyaynen, E.L., Filatova, N.I. and Tchupakhina, N.I. (1996) CO₂-gas-exchange of some vascular plants of polar Ural Mountains (ecological aspect). *Russian J. Plant Physiol.*, 43: 380-390 (in Russian with English summary).
- Gryaz'kin, A.V. and Tarasov, E.V. (1989) Dynamics of soil CO₂-emission depending on environment conditions. *In: Ecology and forest protection. Inter-institute Digest of Papers, S. M. Kirov Forestry Engineering Academy, Leningrad, 16-19 (in Russian).*
- Inoue, G., Maksyutov, S. and Panikov, N. (1995) CO₂ and CH₄ emission from wetlands in west Siberia. *In: Fukuda, M. (ed.) Proc. of the 3rd symposium on the joint Siberian permafrost studies between Japan and Russia in 1994.* Kohsoku Printing Center, Sapporo, Japan, 37-43.
- Ivannikova, L.A., Semenova, N.A. (1988) Daily and seasonal dynamics of CO₂ emanation in a grey forest soil. *Eurasian Soil Science*, 1: 134-139 (in Russian with English summary).
- Landhausser, S.M., Wein, R.W. and Lange, P. (1996) Gas exchange and growth of three arctic tree-line tree species under different soil temperature and drought preconditioning regimes. *Can. J. Bot.*, 74: 686-693.
- Larher, W. (1981) Aims, methods and results of plant-ecological research in mountain ecosystems of Alps. *Bot. J.*, 66: 1114-1134 (in Russian with English summary).
- Limbach, W.H., Oechel, W.C. and Lowell, W. (1982) Photosynthetic and respiratory responses to temperature and light of three Alaskan tundra growth forms. *Holarctic Ecol.*, 5: 150-157.
- Luk'yanova, L.M., Lokteva, T.N. and Bulycheva, T.M.

- (1986) Gas-exchange and pigment system of Kola subarctic plants (Khibiny). Apatity, pp. 126 (in Russian).
- Melekhov, I.S. (1980) Forest science. Moscow, Forest Industry, pp. 408 (in Russian).
- Miroslavov, E.A. (1994) Structural adaptation of plants to cold climate. Bot. J., 79: 20-26 (in Russian with English summary).
- Mori, S., Prokushkin, S.G., Masyagina, O.V., Kajimoto, T., Zyryanova, O.A., Abaimov, A.P., Koike, T., Matsuura, Y., Ueda, R. (1998) Daytime whole-tree respiration under controlled air temperature utilizing heat of permafrost and wood fire in a Siberian larch forest. In: Proceedings of the 6th Symposium on the Joint Siberian Permafrost Studies between Japan and Russia in 1997. Sapporo, Japan. 11-17.
- Nash, T.H., III (ed.) (1996) Lichen biology. Cambridge University Press, Cambridge, UK. 3-11.
- Ponyatovskaya, V.M. (1964) Estimation of abundance and plant distribution in forest ecosystems. Field Geo-botany, 3: 290-299 (in Russian).
- Prokushkin, A.S., Kajimoto, T., Prokushkin, S.G., McDowell, W.H., Abaimov, A.P. and Matsuura, Y. (2005) Climatic factors influencing fluxes of dissolved organic carbon from the forest floor in a continuous-permafrost Siberian watershed. Can. J. For. Res., 35: 2130-2140.
- Prokushkin, S.G., Abaimov, A.P., Prokushkin, A.S. and Kaverzina, L.N. (2002) Nitrogen nutrition of larch stands on permafrost soils in Middle Siberia. Siberian J. Ecol., 2: 203-211 (in Russian with English summary).
- Prokushkin, S.G., Abaimov, A.P., Prokushkin, A.S. and Masyagina, O.V. (2006) Biomass of the soil cover and underbrush in larch associations of the cryolithozone of Middle Siberia. Sib. Ecol. J., 2: 131-139 (in Russian with English summary).
- Raich, J.W. and Schlesinger, W.H. (1992) The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate. Tellus, 44B: 81-99.
- Schulze, E.-D., Wirth, C., Rebmann, C., Vygodskaya, N.N., Kelliher, E.M. and Valentini, R. (1997) Carbon assimilation and growth of pine forest in Central Siberia. In: Abstracts of Workshop on Spatial-Temporal dimensions of high-latitude Ecosystem Change (The Siberian IGBP Transect), V.N. Sukachev Institute of Forest Siberian Branch of Russian Academy of Sciences, Krasnoyarsk, 66: 29-30.
- Schulze, E.-D., Lloyd, J., Kelliher, F.M., Wirth, C., Rebmann, C., Lühker, B., Mund, M., Knohl, A., Milyukova, I., Schulze, W., Ziegler, W., Varlagin, A., Valentini, R., Dore, S., Grigoriev, S., Kolle, O. and Vygodskaya, N.N. (1999) Productivity of forests in the Eurosiberian boreal region and their potential to act as a carbon sink—a synthesis. Global Change Biol., 5: 703-722.
- Semikhatova, O.A. (1968) Characteristics of respiratory gas-exchange of plants. Bot. J., 53: 1069-1084 (in Russian with English summary).
- Semikhatova, O.A. (1995) Maintenance respiration and adaptation of plants. Russian J. Plant Physiol., 42: 312-319 (in Russian with English summary).
- Shuvalova, N.P. (1988) About differences in CO₂-gas-exchange rate of *Perilla ocymoides* (Lamiaceae) leaves during short day period and continuous lighting. Bot. J., 73: 1017-1021 (in Russian with English summary).
- Silvola, J., Alm, J., Ahlholm, U., Nykanen, H. and Martikainen, P.J. (1996) CO₂ fluxes from peat in boreal mires under varying temperature and moisture conditions. J. Ecol., 84: 219-228.
- Wang, Y.P. and Polglase, P.J. (1995) Carbon balance in the tundra, boreal forest and humid tropical forest during climate change: scaling up from leaf physiology and soil carbon dynamics in Amazonia from 1992 to 1993. Plant Cell Environ., 18: 1226-1244.
- Yokota, T. and Hagihara, A. (1996) Seasonal change in the temperature coefficient Q_{10} for respiration of field-grown Hinoki cypress (*Chamaecyparis obtusa*) trees. J. For. Res., 1: 165-168.