

Biogenic Fluxes of Carbon Dioxide in the Old-Growth Spruce Forest in the Middle Taiga: Results of Eddy Covariance Measurements

S. V. Zagirova* and O. A. Mikhailov

Institute of Biology, Komi Scientific Center, Ural Branch, Russian Academy of Sciences, Syktyvkar, 167982 Russia

*e-mail: zagirova@ib.komisc.ru

Received March 31, 2015

Abstract—Fluxes of carbon dioxide in the old-growth bilberry spruce forest in the European Taiga are measured by the eddy covariance technique. A carbon dioxide sink to the ecosystem was observed from April until September; the maximum net-exchange rate of carbon dioxide was recorded in July. During the cold period of the year from October to March, the biogenic flux of CO₂ was directed from the forest canopy to the atmosphere. According to measurements at $u^* > 0.2$, the total annual NEE was 219 g C m⁻²; the annual values of the ecosystem respiration R_{eco} and the gross photosynthesis P_{gross} were 483 and 966 g C m⁻², respectively. The conclusion is that the old-growth bilberry spruce forest in the middle taiga subzone was the sink of carbon from the atmosphere during the year of observation.

Keywords: bilberry spruce forest, carbon dioxide, eddy covariance technique, net-exchange, ecosystem respiration, gross photosynthesis

DOI: 10.1134/S1995425516070106

The role of a forest ecosystem as a carbon sink or a carbon source is determined by the ratio between the rates of carbon dioxide absorption during the photosynthesis of plants and its emission as a result of biota life. The carbon reserves depend on the age of stand and reach their maximum in the old-growth forests that make up a considerable part of unmanaged first-growth forests of the northern hemisphere. In the opinion of a few authors, the old-growth stand from the different climate zones are characterized by a positive carbon balance and can bind about 1.3 Gt C/per yr⁻¹ (Lyussaert et al., 2008). The old-growth forests function as a source of carbon dioxide when they are affected by natural and anthropogenic factors. In the last two decades, the carbon cycle of the land ecosystems has been actively studied by the eddy-covariance technique (Baldocchi et al., 1988). In the territory of Russia, Ukraine, Belorussia, and Kazakhstan, according to the measurements by this technique, the total sink of carbon from the atmosphere to the land ecosystems is estimated at 0.342 Gt C per yr⁻¹, including 90% that belong to the forests, and the net-exchange (NEE) is 1.033 Gt C per yr⁻¹ (Dolman et al., 2012). The main climatic factors that determine the values of gross photosynthesis and respiration in forests of different climate zones is the duration of the warm period and the amount of precipitation (Fernandez-Martinaz et al., 2014). The interannual differences of the net CO₂ exchange in a value and a sign between the forest ecosystem and the atmosphere are

caused by the variability of the air temperature, in the opinion of several authors (Ueyama et al., 2014).

The largest massifs of the old-growth dark coniferous taiga (Aksenov et al., 2003) in Europe are preserved in the Republic of Komi (Aksenov et al., 2003). The carbon reserves in the ecosystems of the old-growth spruce forests of the republic vary within the range of 133–205 t C ha⁻¹ (Manov et al., 2014). The net production of phytomass (NEP) in the bilberry spruce forest of the middle taiga calculated by the weight method amounted to 1.71 t C ha⁻¹ per yr⁻¹, and the quantity of deposited carbon was 3.7 t C ha⁻¹ per yr⁻¹ (Tuzhilkina, Bobkova, 2001). In the bilberry sphagnum spruce forest of the middle taiga, the net sink of carbon is 0.36 t C ha⁻¹ per yr⁻¹ with respect to the production-destructive processes (Kuznetsov, 2010). The purpose of this work was to evaluate the annual dynamics of CO₂ gas exchange in the spruce biogeocenosis with the atmosphere in the middle taiga by the eddy covariance technique.

MATERIALS AND METHODS

The measurements were carried out in 2013 in the old-growth bilberry spruce forest at the Lyalya Forest-Ecological Station of Institute of Biology of Komi Scientific Center of the Ural Branch, Russian Academy of Sciences (62°17' N, 50°40' E). The spruce stand, where the measuring system is mounted, is characterized in (Robakidze et al., 2013). The forest

Measurements of CO₂ fluxes at 30-min intervals for January–December, 2013 excluded from analysis

Period of the year	Reason for exclusion		Used in the statistical analysis
	technical problems	low turbulence	
Jan.–Mar.	1260	441	1803
Apr.–Aug.	58	2027	5259
Sept.–Dec.	749	1074	3211
Total	2067	3542	10273

stand is different-aged, for the V class capacity, with the dominant spruce, other species are also found (7sp2bir1p+asp, fir). No traces of fire or cutting were found in the phytocenosis studied. The height of the spruce and pine trees is 17 m and the aspen trees are 24 m. The age of the spruce trees is 80–180 years. There were 970 growing trees per ha⁻¹ and 303 m³ was the stand of timber per ha⁻¹. Blueberry, huckleberry, shamrock, and startlower are dominant in the grass–low-bush layer. In the moss cover, green mosses prevail. The spruce forest is developed on the podzolic sandy–loam soil overlain by clay loams.

There is also a mixed-herb bilberry spruce forest, a bilberry sphagnum forest, and coniferous–broad-leaved phytocenosis (a bilberry spruce forest, genetically). They are characterized in the monographs (Tuzhilina and Bobkova, 2001; *Korennye...*, 2006). The aspen association occupies a small segment of the spruce forest; we have not found its description in the published literature. These associations could fall into the footprint boundaries, depending on the wind direction and velocity. However, isolating the effect of each association on the calculation of the value of carbon dioxide flux is impossible due to the absence of information on their area and georeference.

The parameters of microclimate (air temperature and humidity, intensity of photosynthetically active radiation (PAR), incident and reflected solar radiation, and radiation balance) were recorded by the automatic meteorostation with the use of CR3000 (Campbell Scientific, United States). The system of studying the CO₂ gas exchange between the ecosystem and the atmosphere by the eddy covariance technique, which is mounted at a height of 30 m, is equipped with an ultrasound anemometer to measure the wind velocity in three projections and the acoustic air temperature (CSAT, Campbell Scientific Inc., United States) and an infrared open-type gas analyzer (EC-150, Campbell Scientific Inc., United States), which makes it possible to obtain the data on the velocity and direction of a vertical flux of CO₂ and H₂O and the thermal-exchange parameters. The data were recorded at a frequency of 20 Hz and were processed by the LoggerNet software (Campbell Scientific, United States).

The software analysis included mathematical and statistical processing of the initial data for 30 min. To continue the work, we selected data with “0” quality index from the array that indicated the stable operation of the gasometric system. The errors in CO₂ exchange measurements could occur due to the following reasons: (1) unstable operation of the system, calibration, replacement of filters and details; (2) insufficient mixing of air at low turbulence; and (3) variation in the environment factors (Foken and Wichura, 1996). In 2013, the technical problems occurred in the system most frequently from September to March (table).

At the next stage, the quality of the selected data was estimated with respect to the dependence of the indices of stability in the atmospheric boundary layer ($z L^{-1}$) and footprint ($d_{fetch70}$) on the dynamic wind velocity (u^*) at the moment of measuring (Fig. 1), as is accepted in measuring by the eddy covariance technique. The analysis of the footprint showed that, in 76% of cases, 90% of the total air flow volume, which was used by the system to calculate the CO₂ flux, was formed at a distance of less than 200 m from the watch tower; in 90% of the cases, the maximum air flow came from a distance of less than 100 m. According to our analysis, the threshold value u^* amounts to 0.2 m s⁻¹ for the data selection; therefore, the values of the CO₂ gas exchange at a lower value of atmospheric turbulence ($u^* < 0.2$ m s⁻¹) were not taken into account later. At the last stage, we removed the emissions that did not conform to reality but were not recorded during the preceding selection of the data. In total, we used 10273 values out of 15882 values recorded for 302 days from January 1 until December 31, 2013. The total diurnal and annual value of the CO₂ gas exchange indices was measured as an integral of the data at a 30-min interval.

An important parameter of measurement quality is closing of the thermal balance equation ($H + L_e = R_n + G$) (Lafleur, 1999). In our studies, the closing of the equation was $(H + L_e) = 1.0969 \cdot (R_n + G) + 5.732$ ($r^2 = 0.88$), which indicates that the quality of the data obtained is quite satisfactory.

The calculated flux of F_{CO_2} carbon dioxide is an equivalent to the net CO₂ exchange (NEE), which is the sum of the gross-photosynthesis (P_{gross}) and the respiration of the ecosystem (R_{eco}). The ecosystem respiration was modeled by the air temperature at the night time according to the regressive equation presented in Fig. 2. The modeling results were extrapolated to estimate R_{eco} in the day time as was done in studying the CO₂ gas exchange in the tundra ecosystems (Zamolodchikov et al., 2003; Kutzbach et al., 2007). P_{gross} was calculated as the difference between the measured NEE value and the modeled ecosystem respiration R_{eco} .

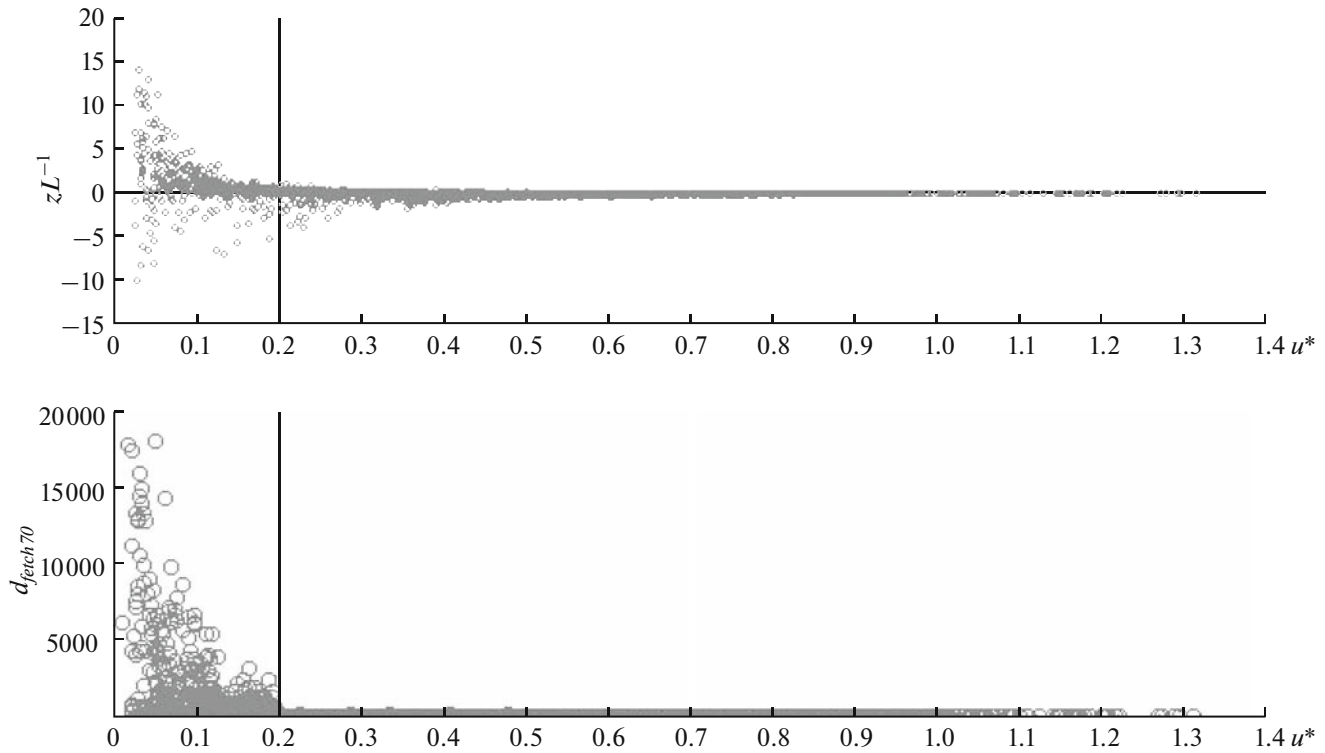


Fig. 1. Dependence of the indices of atmospheric stability in the atmospheric boundary layer (zL^{-1}) and footprint (or the range of influence) ($d_{fetch70}$) on the dynamic wind velocity (u^*). The vertical line shows the critical value of u^* for the selection of CO_2 gas-exchange data.

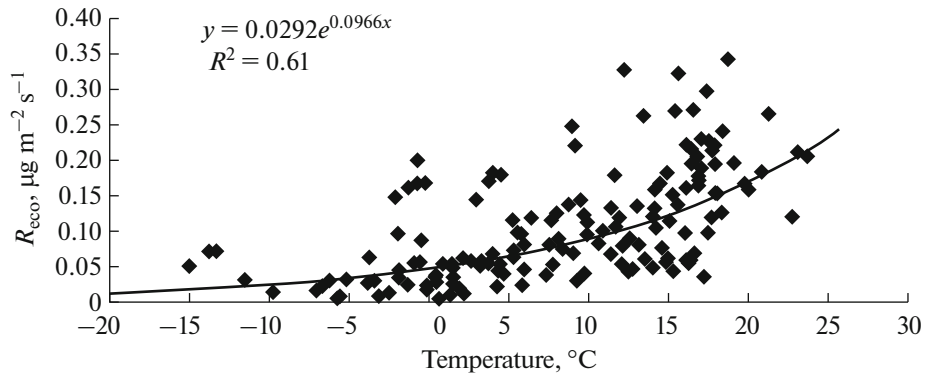


Fig. 2. Air temperature dependence of the average rates of the ecosystem respiration at night time.

RESULTS AND DISCUSSION

Weather conditions. In 2013, January was the coldest winter month in the area under study, when the average diurnal air temperature decreased to $-20^{\circ}C$. The cold weather was maintained until the middle of March. On the first ten days of winter, the average air temperature was $-15^{\circ}C$. The precipitation amount did not exceed 23 mm in the winter months. In the spring, the positive average diurnal temperatures of the atmospheric air were settled after April 13 (Fig. 3). May was relatively warm, the average monthly temperature was $7.3^{\circ}C$, and in June it

reached $14.9^{\circ}C$, which is higher than the average long-term normal value by $1^{\circ}C$. July was hot, especially its first 10 days, with an average monthly air temperature of $17.0^{\circ}C$. In August, the warm weather continued, the average temperature being $14.6^{\circ}C$; in September it decreased to $8.0^{\circ}C$. The first night frosts were recorded at the end of September, and in the second half of October, the steady cold weather was settled in there. The vegetation period when the average diurnal air temperature was above $5^{\circ}C$ lasted for 146 days in 2013. The warm period was noted for a deficit of precipitation; the average monthly pre-

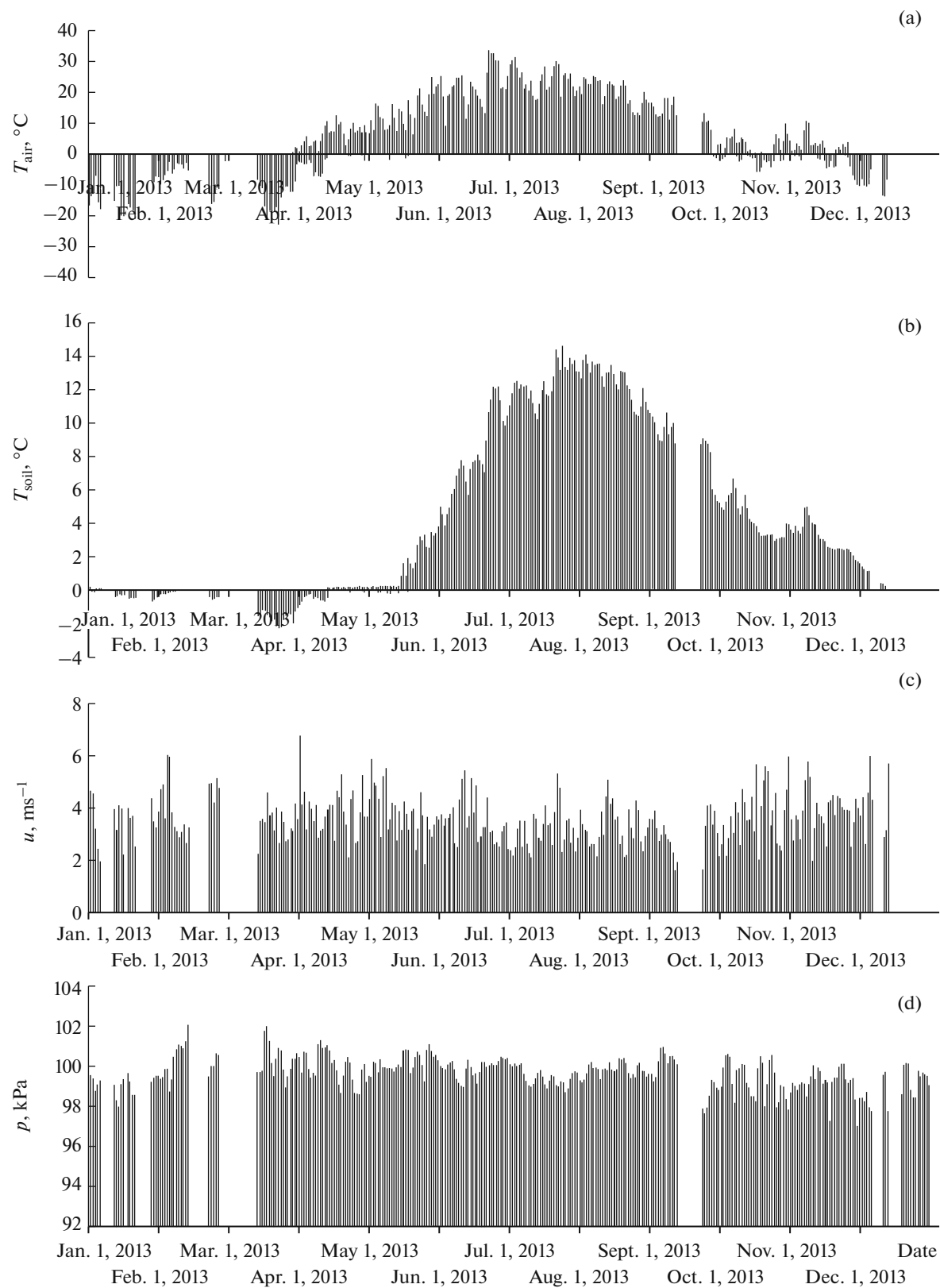


Fig. 3. Meteorological characteristics: (a) is air temperature, (b) is temperature of the litter at a depth of 8 cm, (c) is horizontal wind velocity, and (d) is atmosphere pressure for the bilberry spruce forest in 2013. In Figs. 3–6, dots correspond to the average values at a 30-min measurement interval.

precipitation amount did not exceed 77% of the average long-term normal value in April–August.

The air temperature dynamics is determined by the changes in the temperature regime of the soil during the year. In the spring until the middle of April, the temperature of the litter at a depth of 8 cm in the spruce forest under study was close to zero; it sharply increased starting from May 14, when the air was heated to 15°C during the day. The temperature of the organogenic soil layer had reached 14°C by the end of July and did not go below 10°C in August. It noticeably decreased in September, but remained positive until the end of November.

In the cold period of the year, the horizontal wind velocity increased. During the period of observations its maximum value amounted to 6.7 m s⁻¹. In the warm period of the year, the winds blew from the west (northern, northeastern, and northwestern) and from the south in 56 and 44% of the cases, respectively. The annual atmosphere pressure varied from 99 to 102 kPa (Fig. 3).

Carbon dioxide fluxes. The velocity of the net CO₂ exchange measured by the eddy covariance technique was characterized by the annual dynamics (Fig. 4). In the winter months, during the day *NEE* was positive; i.e., CO₂ was emitted. In the second half of March and the beginning of April, when snow still covered the forest and the air temperature did not rise above 0°C during the day, the average velocity of the CO₂ gas exchange between the forest and the atmosphere reached -0.13 mg CO₂ m⁻² s⁻¹ (i.e., there was a light sink of CO₂); the total *NEE* value during the day was also negative. In the second half of April, as the net-exchange rate and the duration of a light period increased, the total diurnal *NEE* was -4.68 g CO₂ m⁻². The CO₂ gas exchange between the spruce forest and the atmosphere noticeably intensified in May–June, reaching the maximum in July when the period of light and temperature regime was the most favorable for the photosynthesis of woody plants (Fig. 5). In April, the PAR value reached 1000 μmol m⁻² s⁻¹ in the day time on cloudless days, but in July it rose to 1600 μmol m⁻² s⁻¹. The average diurnal intensity of the PAR moving to the upper boundary of the spruce phytocenosis decreased by 20% at the end of August, by 32% in September, and amounted to 45% of the July value in October. The average diurnal temperature decreased almost by 3 times from July to September. The noticeable decrease in the diurnal sink of CO₂ in the spruce forest ecosystem and its return to the emission as early as the beginning of October are likely to have been caused by the changes in these two factors. The data we obtained are consistent with the results of studies that show a close dependence of the spruce photosynthesis rate on the air temperature during the vegetation period (Yuzbekov et al., 2014).

The ecosystem respiration velocity equaled 0.03 μmol CO₂ m⁻² s⁻¹ at the end of March and in early April and grew in May, gradually reaching the maximum (0.74 μmol CO₂ m⁻² s⁻¹ in late June—in July (Fig. 5). There were days when the total value of *R*_{eco} was 30.7 g CO₂ m⁻² per day⁻¹. In August–September, the ecosystem respiration decreased gradually and in October it did not exceed 3 g CO₂ m⁻² per day⁻¹.

The gross photosynthesis value changed in accordance with the dynamics of the net CO₂ exchange, increasing from April until July and gradually decreasing in the cold period of the year (Fig. 5). The maximum total diurnal *P*_{gross} value reached 45 g CO₂ m⁻² in July and decreased by 40% at the end of August, by 55% in September, and amounted to 20% of the July value in October.

Thus, from October until March the bilberry spruce forest was a source of carbon to the atmosphere, and from early April until the end of September it acted as a sink. Despite the negative air temperature at the end of March and early April, there were several days when the net CO₂ exchange rate was close to zero, but with a negative sign. This early return from the emission to the sink of carbon dioxide in the spruce forest could result from the increase in the elevation of the Sun above the horizon, which caused the radiation balance to increase in March by almost four times when compared to February (Fig. 6). Here, the sensible heat flux consumed over 50% of the net radiation, which is likely to have caused the increase in the temperature of aboveground organs, including fir needles. As a result, the temperature became sufficient for the photosynthesis processes in the coniferous plants. According to the available data, photosynthesis can occur in spruce at negative air temperatures, and for its visible photosynthesis the optimal temperature range is < 0–18°C (Drozdov and Kurets, 2003).

The highest value of the carbon dioxide sink in the spruce forest was recorded in the first half of July. The total average diurnal value of *NEE* was 28% in the second half of April, 62% in May, 79% in June, and 31% of the July value in August and September. The active net CO₂ exchange between the ecosystem of the spruce forest and the atmosphere in May–June is likely to be determined by the fact that, in the first half of the summer, the sensible heat flux consumed 70% of the net radiation (our data unpublished), which contributed to the heating of the vegetation layer and the maintenance of the active photosynthesis in coniferous plants. A few authors believe that the maximum value of the net CO₂ exchange in the coniferous forests in May is caused by soil humidity, which is favorable for photosynthesis (Malhi et al., 1999). In the spruce forests of the southern taiga, the high rate of gross photosynthesis was maintained from the middle of May until the middle of July (Olychev et al., 2009).

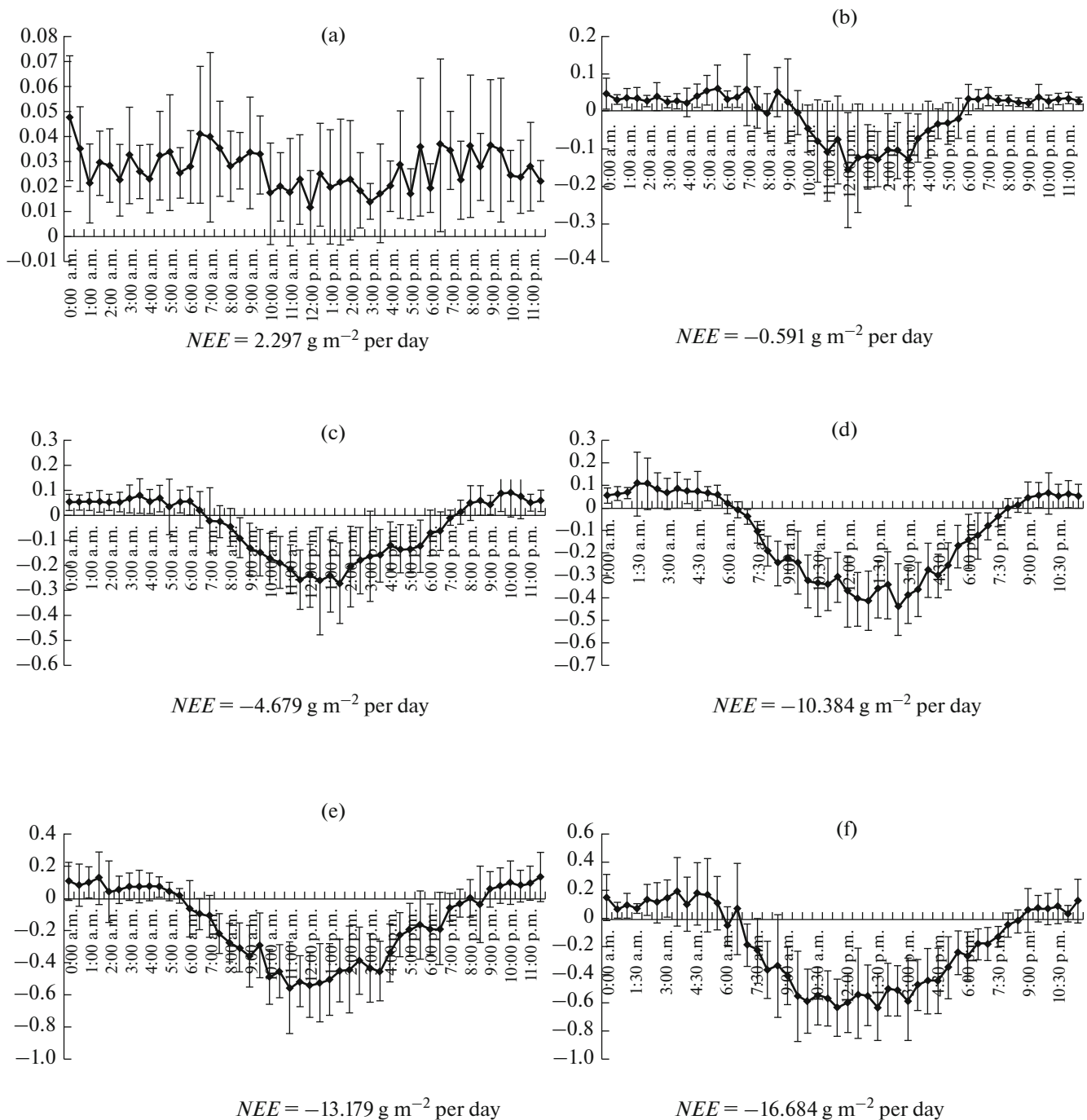


Fig. 4. Average diurnal trends of the net CO_2 gas exchange between the spruce forest ecosystem and the atmosphere in 2013. Bars correspond to the standard deviations. (a) Feb. 1–14, (b) Mar. 16–31, (c) Apr. 15–28, (d) May 1–14, (e) Jun. 1–14, (f) Jul. 1–14, (g) Aug. 1–14, (i) Oct. 1–16, and (j) Nov. 9–22.

The values of the total values of NEE , R_{eco} , and P_{gross} in the bilberry spruce forest we studied were -730 , 1611 , and $3221 \text{ g CO}_2 \text{ m}^{-2} \text{ per yr}^{-1}$ (or -219 , 483 , and $966 \text{ g C m}^{-2} \text{ per yr}^{-1}$), respectively, taking into account the data at $u^* > 0.2$ (Fig. 7). The preceding studies showed that the soil respiration, including the respiration of plant roots, corresponded to 240 – 250 g C m^{-2} in the bilberry-sphagnum spruce forest of

the middle taiga (Kuznetsov and Babkova, 2014). In this case, the annual share of a CO_2 flux emitted from the soil amounts to approximately 57% in the total respiration of the spruce forest respiration. In the southern taiga, the share of soil respiration reaches 70 and 48% of the ecosystem respiration in the spruce-sphagnum forest and in the composite spruce forest, respectively (Olychev et al., 2009).

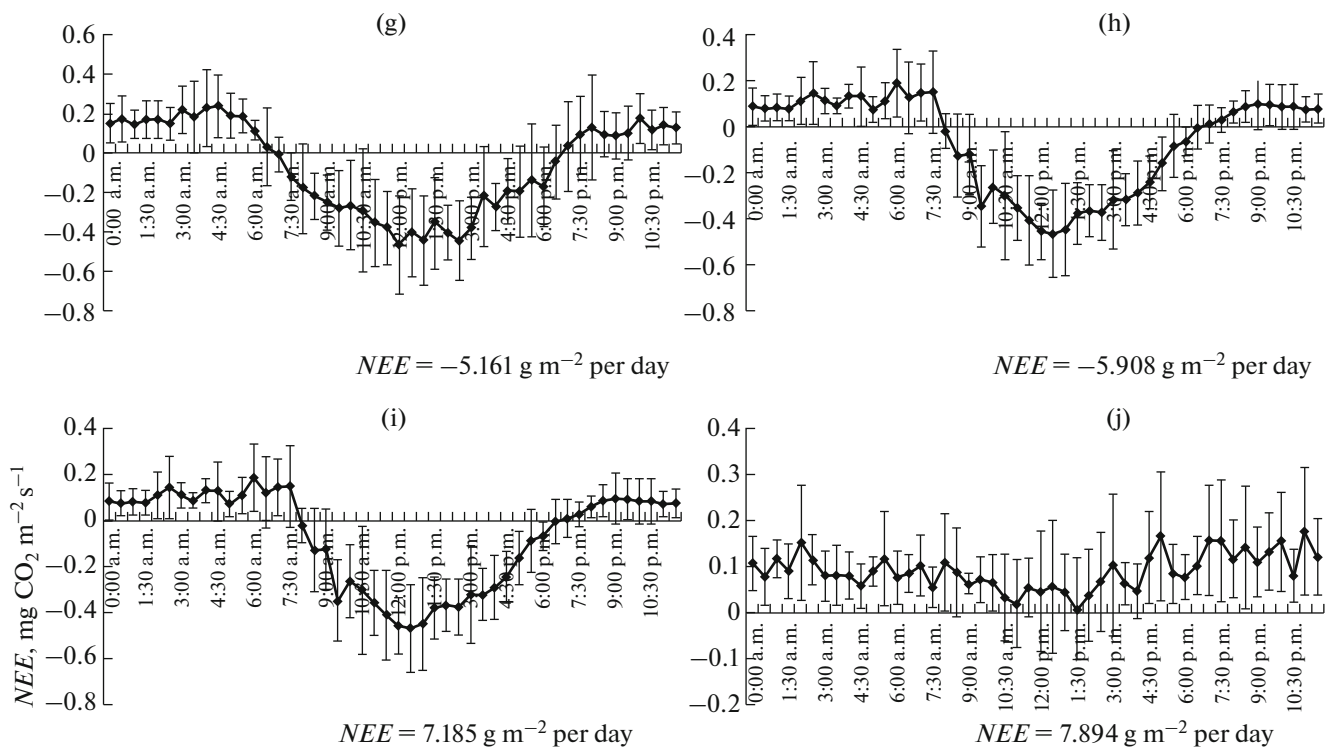


Fig. 4. (Contd.)

The analysis of the available database on the carbon exchange in the forests of different climate zones showed that, in the boreal coniferous forests, 6% of carbon absorbed by the plants (GPP) is stored in NPP leaves, 10% in stems, and 15% in the roots (Fernandez-Martinez et al., 2014), totaling 31%. Taking this distribution into account, the phytomass NPP should be $300 \text{ g C m}^{-2} \text{ per yr}^{-1}$ in the spruce forest studied, which is quite comparable with the value of the primary production obtained by the weight method ($371 \text{ g C m}^{-2} \text{ per yr}^{-1}$) in the bilberry spruce forest in the middle taiga (Tuzhilkina and Bobkova, 2001). The net production of phytomass obtained by the same authors (NEP) for the spruce phytocenosis amounted to 171 g C m^{-2} , which corresponds to 78% of the carbon sink value (NEE) we estimated by the eddy covariance technique. The rest of absorbed carbon is likely to pass to the soil pools of spruce biogeocenosis. In the bilberry–sphagnum spruce forest, the NEE value calculated with respect to the indices of the production–destructive process amounted to $36 \text{ g C m}^{-2} \text{ per yr}^{-1}$ (Kuznetsov, 2010), which is noticeably lower than the value we obtained for the net CO_2 exchange between the ecosystem and the atmosphere by the eddy covariance technique.

In the forest ecosystems of different Russian regions, the NEE value measured by the eddy covariance technique varies from 0 to $-300 \text{ g C m}^{-2} \text{ per yr}^{-1}$

(Dolman et al., 2012). In the southern taiga of the European part of Russia, the composite old-growth spruce forest was served as a sink for $166.5 \text{ g C m}^{-2} \text{ per yr}^{-1}$ (Olychev et al., 2009). However, the total annual values of P_{eco} and P_{gross} calculated by these authors exceeded the values we obtained for the bilberry spruce forest in the middle taiga. In Siberia in the dark coniferous phytocenosis formed by the fir and spruce trees aged 250 years, the carbon sink measured by the same technique amounted to 270 g C m^{-2} during the vegetation period (Röer et al., 2002), and it was 156 g C m^{-2} in the pine phytocenosis (Tchebakova et al., 2015). The lower values of NEE were obtained in the boreal forests of North America. For example, according to the data of measuring a CO_2 gas exchange by the eddy covariance technique in Canada, the carbon sink amounted to $21\text{--}70 \text{ g C m}^{-2} \text{ per yr}^{-1}$ in the old-growth spruce forests affected by a fire more than 100 years ago (Malhi et al., 1999; Amiro et al., 2006) and increased by several times in the mixed 74-year-old coniferous–broad leaved forest, where the total annual values of NEE , R_{eco} , and P_{gross} corresponded to -156 , 919 , and 1075 g C m^{-2} (McGaughey et al., 2006). In total, R_{eco} amounts approximately to 750 g C m^{-2} per year and P_{gross} to 1000 g C m^{-2} per year in the coniferous forests of the boreal zone, and they are noticeably surpassed by the forests in the temperate zone and the tropics (Fernandez-Martinez et al., 2014).

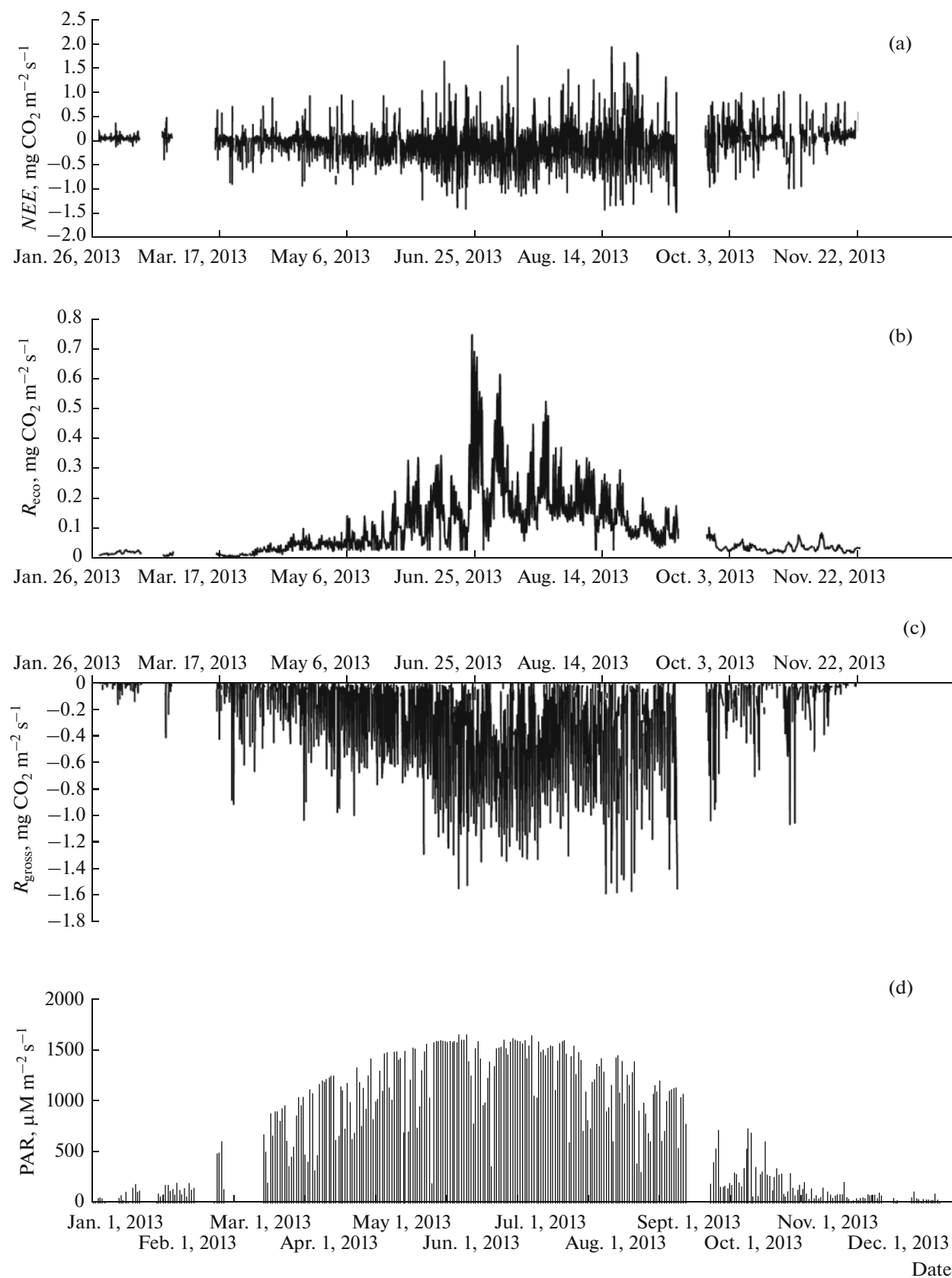


Fig. 5. Annual dynamics of the CO_2 gas exchange and PAR indices in the bilberry spruce forest. (a) CO_2 exchange (NEE), (b) modeled ecosystem respiration (R_{eco}), (c) gross photosynthesis (P_{gross}), and (d) PAR.

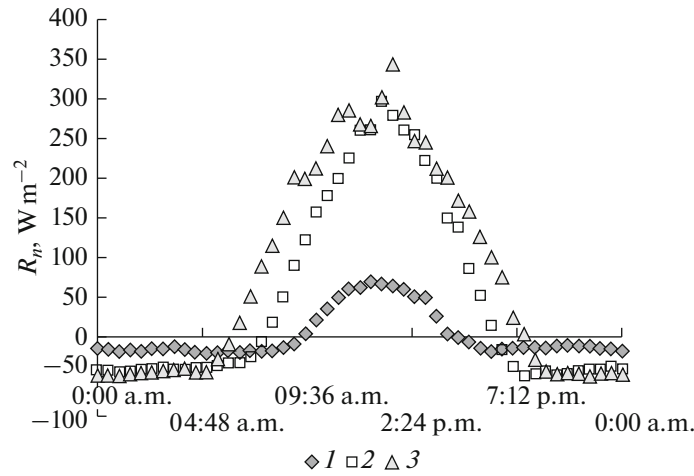


Fig. 6. Diurnal trends of radiation balance (R_r) in the bilberry spruce forest. (1) Feb. 6–20, (2) Mar. 16–31, and (3) Apr. 15–30.

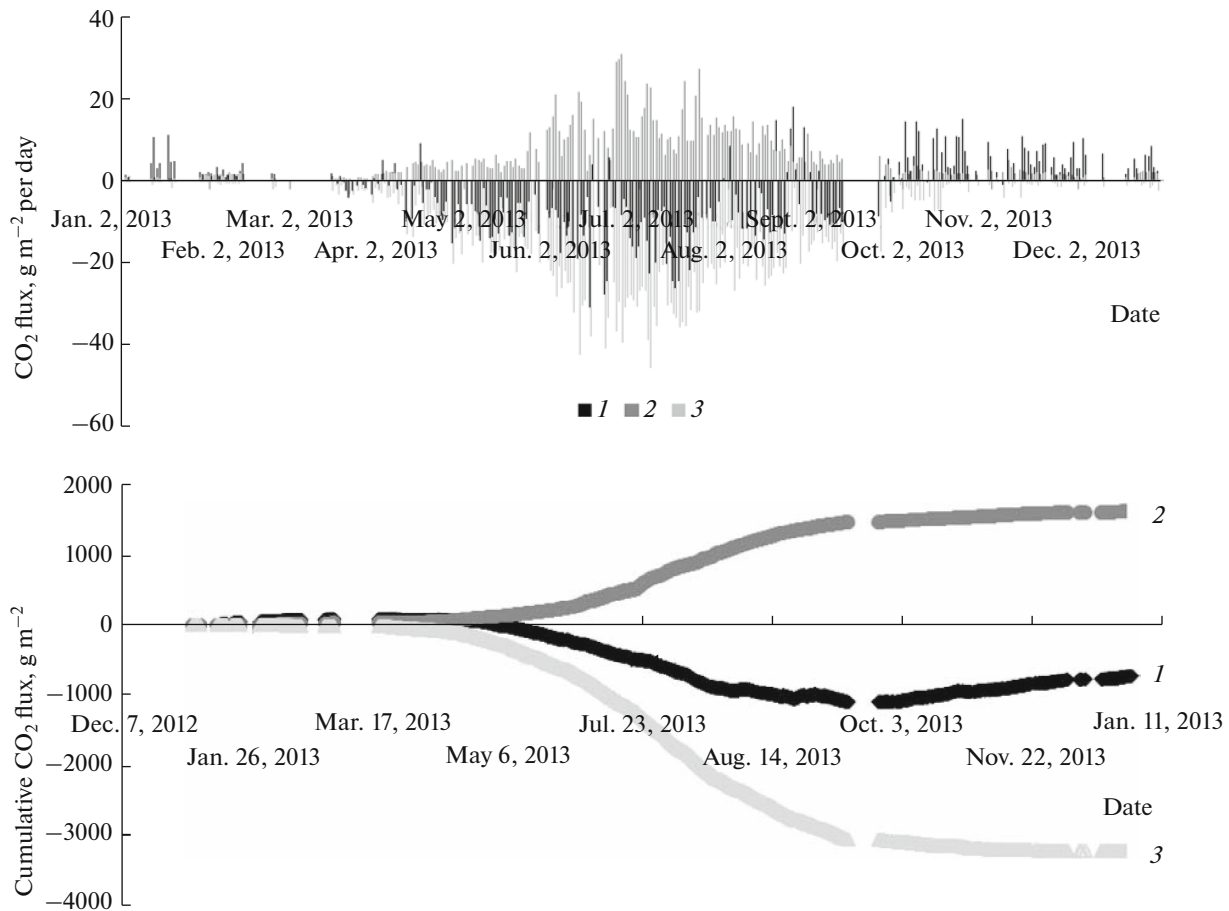


Fig. 7. Daily integrated and cumulative curves CO_2 budget components in the bilberry spruce forest in 2013. (1) NEE , (2) R_{eco} , and (3) P_{gross} .

In the opinion of several authors, the positive balance of the carbon dioxide exchange with the atmosphere is maintained in the forest biogeocenoses aged 200 years or older; its value is approximately

240 g C m^{-2} per yr^{-1} (Lyussaert et al., 2008). However, the total net CO_2 exchange between the forest and the atmosphere in the different years can significantly differ in the value and the sign due to the vari-

ability of the air temperature, primarily in the fall season, as was shown during the long-term measurements at the same spruce forest in Alaska (Ueyama et al., 2014). We note that an increase in the fall temperature leads to the intensification of R_{eco} , which in turn significantly influences the annual CO_2 gas-exchange balance in the ecosystem. In response to the fall increase in the temperature and the intensification of the respiration, the carbon losses can amount to $0.2 \text{ pg C deg}^{-1}$ in the land ecosystems of the northern hemisphere (Piao et al., 2008).

CONCLUSIONS

As a result of measuring the CO_2 gas exchange by the eddy covariance technique, it was established that, in the old-growth bilberry spruce forest of the middle taiga, carbon dioxide is emitted into the atmosphere from October until March; the return from the emission to the sink occurs at the end of March despite the air temperatures still being negative. Photoassimilation of carbon dioxide by coniferous forests is possible in early spring, since the net radiation increases and the large amount of its heat is spent on the sensible heat flux in the spruce forest ecosystem. The net carbon dioxide exchange showed the maximum rate in July, when the temperature and light conditions are the most favorable in the bilberry spruce forest. In general, the value of the carbon sink from the atmosphere to the ecosystem of the bilberry spruce forest obtained during 1 year of observations is comparable with the data obtained using the eddy covariance technique by other authors for the old-growth dark coniferous forests in the boreal zone.

ACKNOWLEDGMENTS

This work was supported by the UNDP/GEF "Strengthening Protected Area System of the Komi Republic to Conserve Virgin Forest Biodiversity in the Pechora Headwaters Region," project no. 00059042.

REFERENCES

- Aksenov, D.E., Dobrynin, D.V., Dubinin, M.Yu., Egorov, A.V., Isaev, A.S., Karpachevskii, M.L., Lestadius, L.G., Potapov, P.V., Purekhovskii, A.Zh., Turubanova, S.A., and Yaroshenko, A.Yu., *Atlas malonarushennykh lesnykh territorii Rossii* (Atlas of Weakly Destroyed Forest Territories of Russia), Moscow: Mezhd. Sots.-Ekol. Soyuz, 2003.
- Amiro, B.D., Barr, A.G., Black, T.A., Iwashita, H., Kljun, N., McCaughey, J.H., Morgenstern, K., Murayama, S., Nestic, Z., Orchansky, A.L., and Saigusa, N., Carbon, energy and water fluxes at mature and disturbed forest sites, Saskatchewan, Canada, *Agric. For. Meteorol.*, 2006, vol. 136, pp. 237–251.
- Baldocchi, D.D., Hincks, B.B., and Meyers, T.P., Measuring biosphere-atmosphere exchanges of biologically related gases with micrometeorological methods, *Ecology*, 1988, vol. 69, no. 5, pp. 1331–1340.
- Bioproduktsionnyi protsess v lesnykh ekosistemakh Severa* (Bioproduction Process in Northern Forest Ecosystems), St. Petersburg: Nauka, 2011.
- Dolman, A.J., Shvidenko, A., Schepachenko, D., Ciais, P., Tchebakova, N., Chen, T., van der Molen, M.K., Belelli Marchesini, L., Maximov, T., Maksyutov, S., and Shulze, E.-D., An estimate of the terrestrial carbon budget of Russia using inventory-based, eddy covariance and inversion methods, *Biogeosciences*, 2012, vol. 9, pp. 5323–5340.
- Drozdo, S.N. and Kurets, V.K., *Nekotorye aspekty ekologicheskoi fiziologii rastenii* (Some Aspects of Ecological Plant Physiology), Petrozavodsk: Petrozavod. Gos. Univ., 2003.
- Fernandez-Martinaz, M., Vicca, S., Janssens, I., Luysaert, S., Campioli, M., Sardans, J., Estiarte, M., and Penuelas, J., Spatial variability and controls over biomass stocks? Carbon fluxes and resource-use efficiencies across forest ecosystems, *Trees*, 2014, vol. 28, pp. 597–611.
- Foken, Th. and Wichura, B., Tools for quality assessment of surface-based flux measurements, *Agric. For. Meteorol.*, 1996, vol. 78, pp. 83–105.
- Korennyye elovye lesa: bioraznoobrazie, struktura, funktsii* (Indigenous Spruce Forests: Biodiversity, Structure, and Functions), St. Petersburg: Nauka, 2006.
- Kutzbach, L., Wille, C., and Pfeiffer, E.-M., The exchange of carbon dioxide between wet arctic tundra and the atmosphere at the Lena River Delta, Northern Siberia, *Biogeosciences*, 2007, vol. 4, no. 5, pp. 869–890.
- Kuznetsov, M.A., Dynamics of organic carbon content in wetland spruce forests in middle taiga, *Extended Abstract of Cand. Sci. (Biol.) Dissertation*, Syktyvkar: Inst. Biol., Komi Sci. Center, Ural Branch, Russ. Acad. Sci., 2010.
- Kuznetsov, M.A. and Bobkova, K.S., Organic carbon fluxes in the system soil-phytocenosis of bilberry-sphagnum spruce forest in the middle taiga zone of the Komi Republic, *Russ. J. Ecol.*, 2014, vol. 45, no. 5, pp. 338–344.
- Laflour, P.M., Growing season energy and CO_2 exchange at a subarctic boreal woodland, *J. Geophys. Res.: Atmos.*, 1999, vol. 104, pp. 9571–9580.
- Luyssaert, S., Schulze, E.-D., Börner, A., Knohl, A., Hessenmöller, D., Law, B., Ciais, P., and Grace, J., Old-growth forests as global carbon sinks, *Nature*, 2008, vol. 455, pp. 213–215.
- Malhi, Y., Baldocchi, D., and Jarvis, P., The carbon balance of tropical, temperate and boreal forests, *Plant, Cell Environ.*, 1999, vol. 22, pp. 715–740.
- Manov, A.V., Osipov, V.M., Osipov, A.F., Kuznetsov, M.A. and Bobkova, K.S., Carbon reserves in forests ecosystems, in *Uglerod v lesnykh i bolotnykh ekosistemakh osobo okhranyaemykh prirodnykh territorii Respubliki Komi* (Carbon in Forest and Wetland Ecosystems of the Strictly Protected Natural Territories of Komi Republic), Syktyvkar: Inst. Biol., Nauch. Tsentra, Ross. Akad. Nauk, 2014, pp. 25–66.
- McCaughey, J.H., Pejam, M.R., Arain, M.A., and Cameron, D.A., Carbon dioxide and energy fluxes from a

- boreal mixedwood forest ecosystem in Ontario, Canada, *Agric. For. Meteorol.*, 2006, vol. 140, pp. 79–96.
- Olychev, A.V., Kurbatova, Yu.A., Tatarinov, F.A., Molchanov, A.G., Varlagin, A.V., Gorshkov, I.I., and Vygodskaya, N.N., Evaluation of primary gross and net production of the spruce forests in the central European part of Russia using the field measurements and mathematical modeling, *Usp. Sovrem. Biol.*, 2009, vol. 129, no. 6, pp. 565–578.
- Piao, S., Ciais, P., Friedlingstein, P., Peylin, P., Reichstein, M., Luyssaert, S., Margolis, H., Fang, J., Barr, A., Chen, A., Grelle, A., Holliger, D., Laurila, T., Lindroth, A., Richardson, A., and Vesala, T., Net carbon dioxide losses of northern ecosystems in response to autumn warming, *Nature*, 2008, no. 456, pp. 49–52.
- Robakidze, E.A., Torlopova, N.V., and Bobkova, K.S., Chemical composition of wet precipitation in old-growth middle-taiga spruce stands, *Geochem. Int.*, 2013, vol. 51, no. 1, pp. 65–75.
- Röser, C., Montagnani, L., Schulze, E.-D., Mollicone, D., Kolle, O., Meroni, M., Papale, D., Marchesini, L.B., Federici, S., and Valentini, R., Net CO₂ exchange rates in three different successional stages of “dark taiga” of central Siberia, *Tellus B*, 2002, no. 54, pp. 642–654.
- Tchebakova, N.M., Vygodskaya, N.N., Arneth, A., Belelli Marchesini, L., Kurbatova, Yu.A., Parfenova, E.I., Valentini, R., Verkhovets, S.V., Vaganov, E.A., and Schulze, E.-D., Energy and mass exchange and the productivity of main Siberian ecosystems (from Eddy covariance measurements). 2. Carbon exchange and productivity, *Biol. Bull.*, 2015, vol. 42, no. 6, pp. 579–588.
- Tuzhilina, V.V. and Bobkova, K.S., Chlorophyll index and annual carbon flux in spruce phytocenosis, in *Bioproduktsionnyi protsess v lesnykh ekosistemakh* (Bioproduction Process in Forest Ecosystems), St. Petersburg: Nauka, 2001, pp. 203–207.
- Ueyama, M., Iwata, H., and Harazono, Y., Autumn warming reduces the CO₂ sink of a black spruce forest in interior Alaska on a nine-year eddy covariance measurement, *Global Change Biol.*, 2014, vol. 20, pp. 1161–1173.
- Yuzbekov, A.K., Zamolodchikov, D.G., and Ivashchenko, A.I., Spruce fir photosynthesis in the forest ecosystems of the Log Tayezhnyi test area, *Moscow Univ. Biol. Sci. Bull.*, 2014, vol. 69, no. 4, pp. 169–172.
- Zamolodchikov, D., Karelin, D., Ivaschenko, A., Oechel, W., and Hastings, S., CO₂ flux measurements in Russian Far East tundra using eddy covariance and closed chamber techniques, *Tellus B*, 2003, no. 55, pp. 879–892.

Translated by L. Mukhortova