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RESEARCH PAPERS

Seasonal Signal of Photosynthesis in the Forests of North Eurasia

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Abstract—The seasonal course of the water potential in branch xylem reflects the dynamics of photosynthetic CO_2/H_2O exchange in the forest stand. Long-term figures of water potential in the branches of major wood species growing in East Siberia—larch (*Larix cajanderi* Mayr), pine (*Pinus sylvestris* L.) and birch (*Betula platyphylla* Sukaczev)—have been analyzed. The seasonal dynamics of the water potential showed its minimum in the first half of the vegetation period. The time when the minimum of water potential was observed concurred with the earlier determined peak in seasonal dynamics of net ecosystem exchange (NEE) of C/CO_2 in the forests of East Siberia. Statistical analysis of a long-term time series of atmospheric CO_2 concentration along the latitudinal zone (43°07′–55°45′ N) of the transcontinental transect from Moscow (55°45′ N, 37°34′ E) to Vladivostok (43°07′ N, 135°54′ E) corroborated the existence of the seasonal minimum of atmospheric CO_2 in the first half of the vegetation period. However, this transcontinental Eurasian minimum of atmospheric CO_2 was reached a month before such a minimum in the region of East Siberia (Yakutsk, 62°05′ N, 129°33′09″ E). It was concluded that the minimum of atmospheric CO_2 concentration is a seasonal signal of photosynthesis in the regional forest ecosystems, and time shift of this signal might serve as an indicator of modification in the regional biogenic cycle of carbon caused by climate fluctuation.

Keywords: Larix cajanderi, *Pinus sylvestris*, *Betula platyphylla*, forests of North Eurasia, photosynthesis, transpiration, water potential, climate fluctuation

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INTRODUCTION

In forest ecosystems, a balance between carbon and oxygen depends on the ratio between photosynthetic reduction of CO_2 to organic matter and reverse oxidative conversion of wood and soil to CO_2. The mission of CO_2 by saprotroph organisms [1] and growth of woody plants [2–4] bear a positive relationship to temperature. Therefore, temperature is one of the major factors for seasonal changes in CO_2 concentration in the atmosphere of the boreal region in the northern hemisphere [5].

Long-term instrumental measurements of atmospheric CO_2 concentration in the forest zone of West Siberia have shown that the seasonal concentration minimum of atmospheric carbon dioxide occurs during the first half of the growing season [6]. This discovery suggested that the restriction of photosynthetic assimilation of CO_2 depends on physiological principles of the production process in woody plants. For instance, it is known that the peaks of NEE [7–9] and evapotranspiration [10–14] occur in the first half of the growing season (June/July) in the larch forests of East Siberia. At the same time, the peak of CO_2 emission flow is reached in July/August (much later than NEE maximum) [15, 16]. These long-term measurements taken in East Siberian larch taiga point to the intensification of CO_2 emission flow and weakening of photosynthetic fixation of CO_2 starting from July. In this case, starting from the second half of the vegetation period, the equilibrium between the flows is attained at a higher content of atmospheric CO_2 on the crown level of cover crop.

It is quite evident that climatic changes will quantitatively and qualitatively modify the natural deposition of carbon and sources of C/CO_2 in the vast Russian biomes. Therefore, the time shift of the minimum CO_2 concentration at a height of the forest stand crown may indicate a reorganization of natural CO_2 flows within forest phytocenoses. There are long-term data concerning seasonal dynamics of the balance between all C/CO_2 flows of cover crop (NEE) in East Siberia

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Abbreviations: NEE—net ecosystem exchange of C/CO_2.

[10–14]. However, information about seasonal photosynthetic activity of forest cover in Eastern Siberia is scarce and fragmentary [17]. In order to determine a relative contribution of photosynthesis to the exhibition of seasonal CO_2 minimum, long-term data describing seasonal dynamics of photosynthetic CO_2/H_2O exchange are also required.

The aim of this investigation was to determine more accurately the contribution of photosynthesis to the attainment of seasonal CO_2 minimum in forest cover of East Siberia and to find out the time when the minimum CO_2 concentration at a height of tree crown averaged for the forest zone along the latitudinal transect of North Eurasia is reached.

MATERIALS AND METHODS

Determining the water potential of xylem sap exuded from branches. The water potential of the fluid exuded by branches was determined in wood species typical of Yakutia: *Larix cajanderi* Mayr, *Pinus sylvestris* L. and *Betula platyphylla* Sukaczev growing not far from Spasskaya Pad' forest station (62°14′ N, 129°37′ E) (Institute of Biological Problems of Cryolithozone, Siberian Branch, Russian Academy of Sciences) from 1995 to 2000.

Preparation of samples for determining the water potential of the xylem exudate. Segments of branches with leaves or needles (8–10-cm-long and 3–5 mm in diameter) from the illuminated part of the crown at a height of 3 m above the ground were cut off with a garden pruner and placed in a dark plastic sack. The water potential of the xylem exudate was determined using a DIK-7000 pressure chamber (Daiki Rika Kogyo Co Ltd., Japan) with a DIK-9222 automatic pressure controller (Daiki Soil & Moisture, Japan) according to a standard technique [18]. A segment of branch with leaves or needles was accommodated in the pressure chamber so that the cut will be on the outside and the outlet embracing the branch segment will be packed with a rubber strip. Using the attached cylinder with compressed air, we increased the pressure in the chamber up to the moment when a drop of exudate appeared from the cut. This pressure was taken as water potential of the xylem sap.

Determination of atmospheric CO_2 concentration. Round-the-clock (15 min apart) measurements of CO_2 concentration in the surface layer at the crown height of the local forest stand were taken using a C20 infrared CO_2 sensor (GSS, United Kingdom) installed on a Carbologic electronic plate (Individual Private Entrepreneur Konovalov Pavel Veniaminovich, Russia). Sensor accuracy was ±2 ppm. Measuring devices were housed in hermetically sealed plastic cases. Each device was accommodated within a laboratory room located on the third or fourth floor of a building not far from the window so that outdoor air will come in at a height of 16–20 m above the ground. Atmospheric air came to the sensor because of passive diffusion along an aluminum tube with an inner diameter of 5 mm extended through the window opening at a distance of 1.5 m. Continuous monitoring of atmospheric CO_2 concentration was carried out in five locations of North Eurasia: Main Botanical Garden, Russian Academy of Sciences (Moscow); Central Siberian Botanical Garden, Siberian Branch, Russian Academy of Sciences (Novosibirsk); Federal Scientific Center of the East Asia Terrestrial Biodiversity, Far East Branch, Russian Academy of Sciences (Vladivostok); Institute of Biological Problems of the Cryolithozone, Siberian Branch, Russian Academy of Sciences (Yakutsk-I); and Spasskaya Pad' Biological Station, Institute of Biological Problems of the Cryolithozone, Siberian Branch, Russian Academy of Sciences (Yakutsk-II) (Fig. 1). Rather coarse CO_2 sensors isolated seasonal atmospheric signal of photosynthesis on the condition that incidental background fluctuations of atmospheric CO_2 were filtered. Such a screening was ensured by a considerable geographic remoteness of the sensors performing simultaneous and continuous, year-round monitoring of atmospheric concentration of CO_2 and monthly averaging of many thousands of measurements. For the purposes of our investigation, it was important to determine the calendar period when atmospheric content of CO_2 reached its minimum. Besides, change-over from absolute atmospheric CO_2 concentrations to relative values made it possible to do without expensive and time-consuming monthly calibration of the sensors by absolute concentrations of CO_2 and to bring the measurements taken with different sensors in different locations into comparable form.

Climatic characteristics of the locations where atmospheric concentration of CO_2 was measured. Moscow: average daytime temperature is 3.6°C, average air temperature during the vegetation period (May–September) is approximately 14°C, total precipitation is 325 mm, average minimum air temperature in winter is –7.1°C [19]. **Novosibirsk:** average daytime temperature is –0.2°C, average air temperature during the vegetation period (May–September) is approximately 14°C, total precipitation is 273 mm, average minimum air temperature in winter is –12.3°C [19]. **Vladivostok:** average daytime temperature is 3.9°C, average air temperature during the vegetation period (May–September) is approximately 15°C, total precipitation is 721 mm, average minimum air temperature in winter is –8.2°C [19]. **Yakutsk:** average daytime temperature is –10.2°C, average air temperature during the vegetation period (May–September) is approximately 12.2°C, total precipitation is 213 mm, average minimum air temperature in winter is –26.2°C [19].

Statistical analysis of time series of atmospheric CO_2 concentration. For each region and year, average monthly values of atmospheric concentration of CO_2 were expressed as a dimensionless quantity: a result of division of this value by the minimal for this year and location concentration of CO_2. After that, dimension-

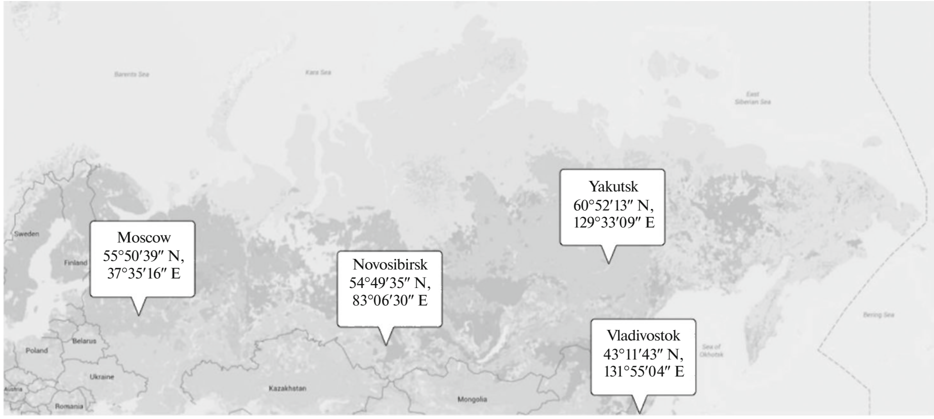

Fig. 1. Map of locations where atmospheric CO_2 was monitored along the transcontinental transect of North Eurasia.

less quantities were consolidated to form two data files: (1) the city of Yakutsk (Yakutsk-I) and Spasskaya Pad' biological station (Yakutsk-II) and (2) the Moscow–Novosibirsk–Vladivostok transcontinental zone. These two data files of month/CO_2 concentration pair matching were arranged in equal rank intervals from smaller to greater values of CO_2 concentration. All the values from the first two rank intervals were taken as the least values of the whole data file. Frequency of occurrence of each month in these first two rank intervals reflected the probability that this month will prove to be the month with the lowest value of CO_2 atmospheric concentration.

RESULTS

Figure 2 shows the results of long-term determinations of the xylem water potential in detached branches of edificatory wood species of East Siberia: larch, birch, and pine. For all the examined species, minimum values of xylem water potential were detected in late June, i.e., during the first half of the vegetation period.

Use of rather cheap CO_2 sensors makes it possible to select an atmospheric seasonal signal of photosynthesis on the condition that concomitant background fluctuations of atmospheric CO_2 are filtered. Statistic parameters of the sample of average monthly values of CO_2 recorded in different months of different years in different locations are shown in Table 1. In respect to the whole data file (Table 1), we employed two-factor analysis of variance by geography (location of CO_2 sensor) and season (calendar month). The results of two-way analysis of variance of the whole data file are shown in Table 2. With a high degree of reliability ($P > 0.01$), we found that in respect to geographic factor, a null statistical hypothesis is rejected. Therefore, geographical location is a significant factor affecting average monthly atmospheric concentration of CO_2. In respect to seasonal factor, we failed to reject a null statistical hypothesis at the marginally significant confidence level. Thus, in respect to seasonal factor for the whole data file of long-term observations, we can conclude that they obeyed a random normal distribution.

In order to bring the seasonal course of atmospheric CO_2 concentration observed in different years in different locations (Table 1) to a comparable form, initial data files were pretreated. Firstly, for each region and year, average monthly values of atmospheric CO_2 concentration were expressed as a dimensionless quantity resulting from division of this value by the lowest for this year and location concentration of CO_2. The components of the whole data file of average monthly values were then consolidated and arranged as a series ordered from the minimum to the maximum value. Secondly, the ordered series of the consolidated data file concerning the city of Yakutsk and Spasskaya Pad' biostation was partitioned into 35 equal rank intervals (Fig. 3a). For the southern transcontinental zone of Northern Eurasia, the data were split into 40 intervals (Fig. 3b). Two lower ranks of each data file contained approximately half of all the data (Fig. 3). Since each value of atmospheric CO_2 concentration is associated with a specific calendar month, the whole data file is an associative series of month/atmospheric CO_2 concentration pairs (Table 1). Therefore, we assumed that the frequency of occurrence of one or another month among the values from the two lower ranks reflects the probability that this month will prove to be the month with the lowest concentration of CO_2. Figure 4 shows this probability for all the calendar months. Statistical analysis of the whole associative series of month/atmospheric CO_2 concentration pairs from the two lower rank intervals has shown that, within North Eurasia (Fig. 1), the seasonal minimum of atmospheric CO_2 concentration in Central Yakutia is most probable in May (Fig. 4a), while it is in April in the southern taiga transcontinental zone (Fig. 4b).

DISCUSSION

The most widespread species in East Siberia is larch, which occupies more than 95% of the woodland. The proportion of pine forests is not very great. Compact

Table 1. Annual dynamics of CO_2 concentration in the atmosphere at a height of crown space of woodland in different regions of North Eurasia

Year	Month	Moscow		Novosibirsk		Vladivostok		Yakutsk-I		Yakutsk-II	
		CO_2, ppm	*n*	CO_2, ppm	*n*	CO_2, ppm	*n*	CO_2, ppm	*n*	CO_2, ppm	*n*
2009	11	–	–	379	645	–	–	–	–	–	–
2009	12	377	668	379	2248	–	–	–	–	–	–
2010	1	378	4536	–	–	–	–	–	–	–	–
2010	2	378	4099	–	–	–	–	–	–	–	–
2010	3	379	2974	377	4487	–	–	–	–	–	–
2010	4	379	4393	377	4372	–	–	–	–	–	–
2010	5	380	4527	377	1142	–	–	–	–	–	–
2010	6	381	4391	377	4378	–	–	–	–	–	–
2010	7	381	1221	378	4522	–	–	–	–	–	–
2010	8	380	1069	382	4523	–	–	–	–	–	–
2010	9	380	4373	382	4384	–	–	–	–	–	–
2010	10	380	4109	383	4504	376	2107	–	–	–	–
2010	11	380	4367	383	4380	376	4393	–	–	–	–
2010	12	380	4512	382	4531	377	4536	–	–	–	–
2011	1	380	4515	382	4531	377	4514	–	–	–	–
2011	2	380	4081	383	4094	377	4100	–	–	–	–
2011	3	380	4517	382	4511	377	4542	–	–	–	–
2011	4	380	4374	382	4392	377	4381	–	–	–	–
2011	5	380	4521	382	3815	377	4544	–	–	–	–
2011	6	381	4379	381	4395	377	4359	–	–	–	–
2011	7	383	4531	381	4540	377	4542	–	–	–	–
2011	8	383	4524	381	4539	378	4536	–	–	–	–
2011	9	384	2349	381	3664	378	4114	–	–	–	–
2011	10	384	3551	375	4034	377	4514	–	–	–	–
2011	11	387	212	378	3362	377	4384	378	16394	377	2057
2011	12	388	2914	378	4538	377	4533	377	20809	376	794
2012	1	384	2973	379	4536	377	4536	377	19364	376	1225
2012	2	383	2754	379	4245	377	4243	377	20649	376	2777
2012	3	382	2974	378	4537	379	4539	377	22146	376	2722
2012	4	381	2877	377	4398	377	4390	377	9363	376	2233
2012	5	377	1578	377	4547	378	4534	378	22098	376	2970
2012	6	377	2371	376	2514	378	3948	378	21254	376	2871
2012	7	375	2107	–	–	–	–	379	2492	376	169
2012	8	379	2365	–	–	–	–	379	1363	–	–
2012	9	382	2514	379	3327	379	13674	380	4182	–	–
2012	10	380	2510	378	4665	383	30175	379	4133	–	–
2012	11	381	1582	377	4514	386	28840	378	1661	–	–
2012	12	385	2970	376	4661	387	30486	379	4251	–	–

Table 1. (Contd.)

Year	Month	Moscow		Novosibirsk		Vladivostok		Yakutsk-I		Yakutsk-II	
		CO_2, ppm	*n*	CO_2, ppm	*n*	CO_2, ppm	*n*	CO_2, ppm	*n*	CO_2, ppm	*n*
2013	1	384	2917	377	4662	384	29732	379	4248	–	–
2013	2	382	2601	377	4211	381	24275	380	3840	–	–
2013	3	380	2880	377	4667	–	–	379	4251	–	–
2013	4	379	2787	377	4511	–	–	379	4113	–	–
2013	5	379	2879	377	4667	378	7793	379	4236	–	–
2013	6	378	2783	377	4518	377	27857	380	4110	–	–
2013	7	375	2871	377	4671	374	29370	381	4251	–	–
2013	8	378	2902	378	4666	369	14737	382	2552	–	–
2013	9	380	2787	377	4512	367	23260	384	4088	–	–
2013	10	378	2880	378	4666	375	17018	383	4248	–	–
2013	11	378	2815	377	4508	376	28607	383	4114	–	–
2013	12	381	2959	377	4667	378	7803	382	4251	–	–
2014	1	380	2880	377	4666	380	14954	383	4250	–	–
2014	2	382	2601	376	4214	377	28193	385	3840	–	–
2014	3	379	2880	377	4667	371	29965	385	4251	–	–
2014	4	381	2787	377	4518	369	21126	385	4075	–	–
2014	5	378	2879	376	4666	377	29094	382	4251	–	–
2014	6	377	2787	377	4515	369	31835	382	4109	–	–
2014	7	375	2880	377	4671	368	25486	383	4251	–	–
2014	8	375	2912	377	4669	366	11349	384	4249	–	–
2014	9	376	2840	377	4377	366	5346	385	4111	–	–
2014	10	377	1451	378	4664	371	4501	386	3030	–	–
2014	11	–	–	377	4517	370	4503	387	2778	378	1305
2014	12	–	–	377	4665	371	4660	388	2879	378	4535
2015	1	–	–	–	–	371	4644	387	2880	378	4536
2015	2	–	–	–	–	371	4196	386	2601	378	4098
2015	3	–	–	–	–	370	4661	387	2880	378	4539
2015	4	–	–	–	–	370	4512	388	2783	378	4397
2015	5	–	–	–	–	370	4650	385	1058	378	4539
2015	6	–	–	–	–	371	4493	380	1739	377	4302
2015	7	–	–	–	–	371	4665	379	2871	377	4511
2015	8	–	–	–	–	371	4666	379	2878	377	4442
2015	9	–	–	–	–	371	4499	384	2787	377	4384
2015	10	–	–	–	–	372	4663	384	2880	377	4540
2015	11	–	–	–	–	373	4456	387	2785	378	4387
2015	12	–	–	–	–	373.	4533	392	2880	378	4535
2016	1	–	–	–	–	373	4656	392	2879	378	4536
2016	2	–	–	–	–	373	4341	392	2694	378	4241
2016	3	–	–	–	–	372	4659	390	2880	378	4540
2016	4	–	–	–	–	372	4509	388	2779	378	4392
2016	5	–	–	–	–	372	4656	388	2876	378	9196
2016	6	–	–	–	–	373	4477	384	2785	–	–
2016	7	–	–	–	–	372	1674	384	963	–	–

The means and the number of measurements taken during the month (*n*) are shown. Dash designates no data.

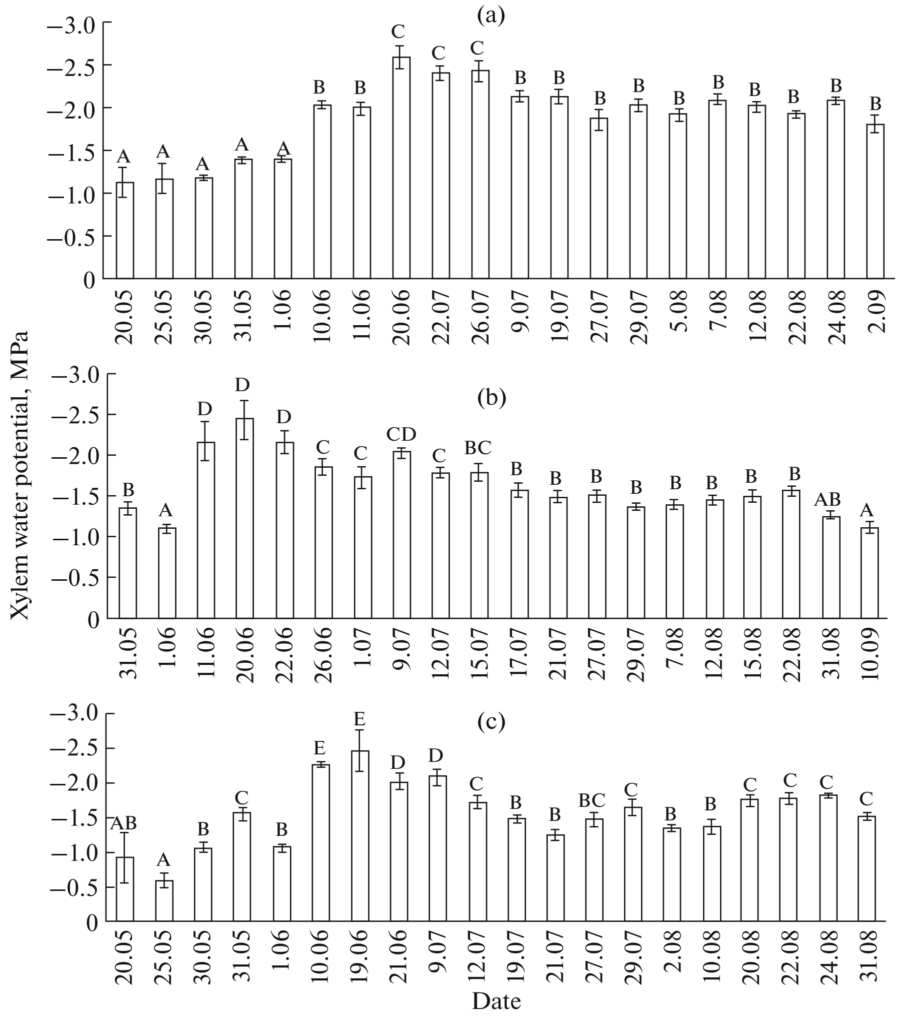

Fig. 2. Seasonal course of changes in xylem water potential of leafed branches of (a) larch, (b) birch, and (c) pine at Spasskaya Pad' biostation near the city of Yakutsk in East Siberia.

pine forests typically occupy dry heights with sandy soils. Birch is a minor component of taiga association; as a pioneer species, it first settles in fire-sites and clearings moving far north as a component of forest–tundra plant associations. Therefore, it is quite reasonable to employ these wood species as edificators in East Siberia.

In respect to East Siberia, there are reports about synchronous seasonal changes in the transpiration of the forest ecosystem and its NEE [10, 11, 17, 20]. A direct relationship between photosynthesis and water translocation depends on a close coupling of photosynthetic CO_2 assimilation with transpiration in the course of CO_2/H_2O exchange of the leaf. In turn, a reduction in xylem water potential implies intensification of water delivery from the soil to plants, i.e., activation of transpiration and photosynthesis. Thus, the time course of the

Table 2. Statistical parameters of the data file of atmospheric CO_2 concentration

Factors	Total sum of squares (D)	Degrees of freedom	Variance	F_{actual}	F_{st}	
					0.05	0.01
Total (y)	5319.1	267	19.9	1.1	1.2	1.3
Geographical (A)	2245.1	4	561.3	31.1	2.4	3.4
Seasonal (B)	151.9	11	13.8	0.8	2.5	3.7
Interaction (AB)	229.6	44	5.2	0.3	1.5	1.8
A + B + AB	2626.7	59	44.5	2.5	1.4	1.7
Remainder variation (z)	2692.4	149	18.1			

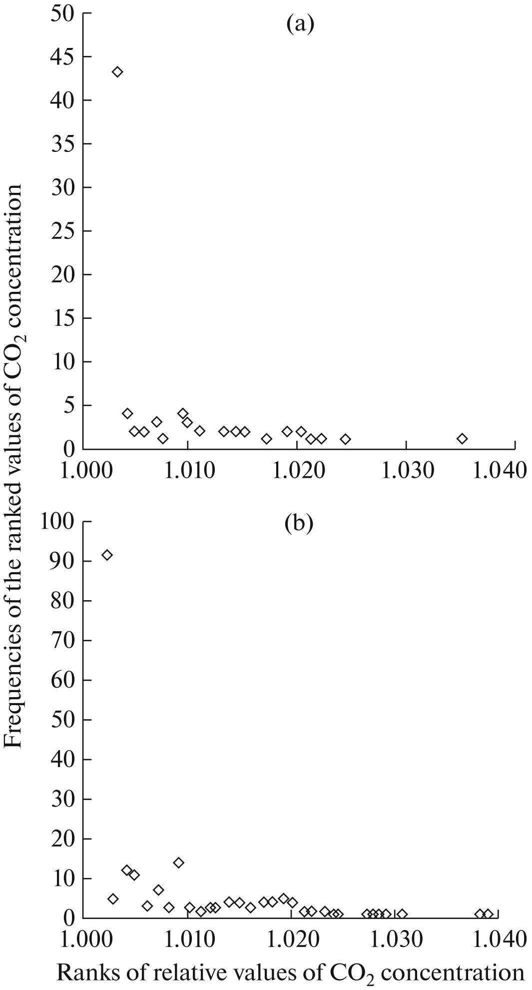

Fig. 3. Ranking of normalized data file concerning atmospheric CO_2 concentration (a) in the city of Yakutsk and at Spasskaya Pad' biostation and (b) along Moscow–Novosibirsk–Vladivostok transect in North Eurasia.

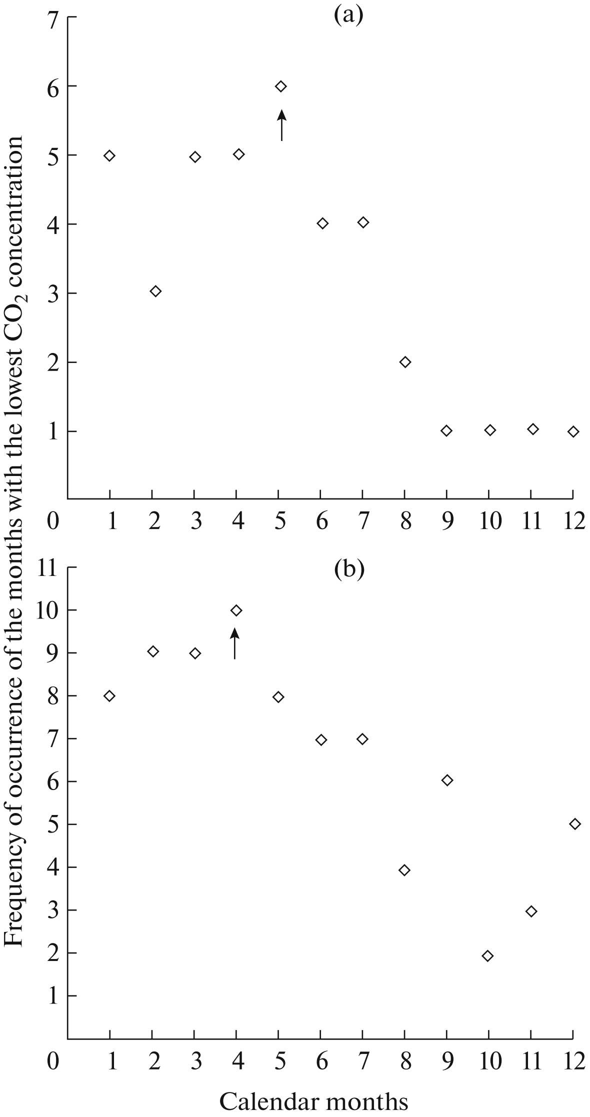

Fig. 4. Distribution of frequencies of occurrence of the months with the lowest concentration of atmospheric CO_2 within the data file concerning (a) the city of Yakutsk and Spasskaya Pad' biostation near Yakutsk and (b) along Moscow–Novosibirsk–Vladivostok transect in North Eurasia. Arrows show the greatest values of the frequencies of occurrence for the months in the month/atmospheric CO_2 concentration associative series in the rank interval comprising the lowest values of atmospheric CO_2.

xylem water potential reflects seasonal changes in photosynthetic assimilation of CO_2 by the forest stand. Judging from the seasonal dynamics of xylem water potential of branches, the photosynthetic function reaches its peak in late June–early July (Fig. 2), which concurs with the seasonal maximum of cover crop evapotranspiration [7–9]. At the same time, during the first half of the vegetation period, CO_2 emission of tree phytocenosis is distinctly behind its photosynthesis [15, 16].

The magnitude of the seasonal lagging of CO_2 emission behind photosynthesis depends on temperature and moisture conditions of the soil and physiological peculiarities of the production process in trees. It is well known that photosynthesis may be restricted under normal natural conditions by the demand for photoassimilates from growing organs and tissues [21].

In turn, the demand for photoassimilates within woody plants causes redistribution of photosynthetic carbon from a slowly oxidized storage pool to rapidly oxidized growth pool [22]. When parity between photosynthesis and respiration is achieved in the second half of the vegetation period, it restricts the deposition of photosynthetic carbon in the ecosystem. Thus, in larch taiga of East Siberia, the concentration minimum of atmospheric CO_2 observed in the first half of the vegetation period depends on a combination of seasonal maximum of the photosynthetic function of vegetation reached by July (Fig. 3) and lagging rise in soil temperature, which is a driver of CO_2 emission in the ecosystem [15, 16]. The analysis of long-term time series describing CO_2 concentration in the atmosphere along the latitudinal transect of North Eurasia (Fig. 1) corroborated the seasonal minimum of CO_2 in the first half of the vegetation period (Fig. 4). Climatic conditions along the latitudinal transect of North Eurasia are much milder than the regional climate of Central Yakutia. The average annual temperature along the latitudinal transect of North Eurasia is by 1.5–2°C higher than in Central Yakutia (see MATERIALS AND METHODS). We discovered that the seasonal minimum of CO_2 occurred at earlier dates in this transcontinental zone of the southern taiga than in the forests of Central Yakutia (Fig. 4).

Thus, the seasonal course of atmospheric CO_2 concentration adequately reflects changes in the ratio between photosynthesis and CO_2 emission and may be used as an indicator of regional modification of the biogenic carbon cycle in forest ecosystems upon climate fluctuation.

COMPLIANCE WITH ETHICAL STANDARDS

This article does not contain any studies involving animals or human participants performed by any of the authors.

CONFLICT OF INTERESTS

The authors declare that they have no conflict of interests.

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