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Partitioning of ecosystem respiration in a paludified shallow-peat spruce forest in the southern taiga of European Russia

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Abstract

Soil, tree stems, and ecosystem carbon dioxide fluxes were measured by chambers and eddy covariance methods in a paludified shallow-peat spruce forest in the southern taiga of European Russia (Tver region, 56°N 33°E) during the growing seasons of 2002–2012. The site was established in 1998 as part of the EUROSIBERIAN CARBONFLUX project, an international field experiment examining atmosphere–biosphere interaction in Siberia and European Russia. In all years the observed annual cumulative net ecosystem flux was positive (the forest was a source of carbon to the atmosphere). Soil and tree stem respiration was a significant part of the total ecosystem respiration (ER) in this paludified shallow-peat spruce forest. On average, 49% of the ER came from soil respiration. We found that the soil fluxes exhibited high seasonal variability, ranging from 0.7 to 10 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Generally, the soil respiration depended on the soil temperature and ground water level. In drought conditions, the soil respiration was low and did not depend on temperature. The stem respiration of spruces grew intensively in May, had permanently high values from June to the end of September, and in October it dramatically decreased. The tree stem respiration in midsummer was about 3–5 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for dominant trees and about 1–2 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for subdominant trees. The respiration of living tree stems was about 10–20% of the ER.

Keywords: CO₂ fluxes, paludified spruce forest, tree stem respiration, soil respiration

1. Introduction

Generally, boreal and subarctic peatlands are, per area, one of the largest storages of soil carbon, and they are

estimated to store between 350 and 535 Gt carbon (Gorham 1991). Ecosystem respiration (ER) is the largest carbon flux from peatlands to the atmosphere (Mäkiranta *et al* 2008, Raich and Schlesinger 1992). The decomposition of organic matter in northern peatlands is limited by several environmental factors, including low temperatures, low pH, oxygen limitation of oxidase activity, functionally limited decomposer communities, and low nitrogen content (Freeman



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et al 2001, Moore and Basiliko 2006, Weedon et al 2013). These constraints have led to a long-term accumulation of organic matter. This large C store is vulnerable to any change of climate which alleviates any of the current constraints on decomposition (Gorham 1991). Peatland can be both a sink as well as a source of carbon dioxide, depending on the temperature and moisture conditions (Arneeth et al 2002, Kurbatova et al 2009). Therefore, the production and consumption of greenhouse gases in peat soils is highly dependent on the oxygen availability in the soil and, thus, the depth of the water table (Martikainen et al 1993, Aerts and Ludwig 1997).

Over one third of all world peatlands are located in Russia (www.imcg.net). Peatlands have been estimated to cover over 8% of the country, or over 20% of the country when combined with paludified shallow peatlands (the peat layer is less than 30 cm), with which they are ecologically close and hardly separated spatially. Woody vegetation covers about 38% of the peatlands area and about 47% of paludified lands (Vompersky et al 2011). The presence of woody vegetation contributes to better drainage of such lands, preserving the general trend of waterlogging. The rate of carbon dioxide (CO₂) emission from peatlands and shallow peatlands varies by orders of magnitude, depending on ecological characteristics, geographic position, and anthropogenic transformation of boggy landscapes.

According to recent estimates, soil efflux (R) represents from 42 to 76% of the ER (Wang et al 2004, Hamilton et al 2002, Law et al 1999, Lavigne et al 1997, Goulden et al 1996). However, the respiration of above-ground woody biomass (R_w) also plays an important role in the total carbon balance of terrestrial ecosystems. The contribution of CO₂ emission from the surface of tree stems is estimated to be from 5 to 22% of the total carbon balance of forest ecosystems (Shibistova et al 2002, Wang et al 2004, Zha et al 2004, Law et al 1999, Lavigne et al 1997, Goulden et al 1996, etc). While the contributions of R and R_w to the ER have previously been investigated in forest ecosystems, these have not been widely explored in shallow-peat forest ecosystems.

In the present study, we examined CO₂ efflux from tree stems and soil in a central Russian *Sphagnum-Vaccinium myrtillus* paludified shallow-peat spruce forest over several growing seasons.

The site was established in 1998 as a spruce forest site of the EUROSIBERIAN CARBONFLUX project, an international field experiment examining atmosphere–biosphere interactions in Siberia and European Russia (Schultze et al 2002). Previous work has shown the site to be a persistent and significant source of carbon to the atmosphere (Milyukova et al 2002, Kurbatova et al 2008). Chamber measurements of soil and wood respiration were also conducted in the forest from 2002 to 2012 (Molchanov et al 2011a, 2011b, Tatarinov et al 2011). Respiration data obtained mostly during a one-week field campaigns were applied for estimating the dependence of soil and stem CO₂ fluxes on the environmental factors, up-scaling of the results to the stand level, and their comparison with continuous eddy covariance data records. The main goals of our present study were to (1) estimate

the dependence of the CO₂ efflux from soil and wood on environmental factors and tree characteristics using the most complete dataset of our measurements (as the results from recent years were not included in earlier studies) and (2) combine chamber and eddy covariance measurements in order to evaluate the contribution of soil and wood in the total ecosystem respiration in a paludified spruce forest.

2. Methods

2.1. Site location and description

The study area is located at 56°N, 33°E, in central European Russia, within the Central Forest State Natural Biosphere Reserve (CFSNBR). A detailed description of the physical geography features of the site is presented in Vygodskaya et al (2002) and Schultze et al (2002). The CFSNBR is situated in the Southern Valdai upland on the main watershed of the Russian Plain. The climate of the area is temperate and moderately continental, with an annual mean temperature of 3.8 °C and annual precipitation of 731 mm. The precipitation mainly occurs during the May–September period, accounting for 381 mm ± 101.5 mm (Minayeva et al 2001). The frost-free period is 111 days on average. The forest under study is situated in a shallow depression. The territory is rather heterogeneous and represents the *Sphagnum-Vaccinium myrtillus* community on peaty soil. The water table reaches the soil surface in spring, and during summer its depth is generally about 26 cm ± 19 cm. The forest is characterized by poor soil aeration, low pH (3.5–3.8), and low nitrogen content (0.5–9.9 kg ha⁻¹). The ground flora is dominated by *Vaccinium myrtillus* and a moss layer of *Sphagnum girgensohnii* and *S. magellanicum*. The forest stand is 170–180 years old and has an average above-ground wood volume of 300 m³ ha⁻¹. The forest is composed of 86% Norway spruce (*Picea abies* (L.) Karst) and 14% birch (*Betula pubescens* L.), with a small admixture of Scots pine (*Pinus sylvestris* L.).

2.2. Measurements and statistics

Continuous eddy covariance measurements of carbon dioxide fluxes and associated environmental parameters have been conducted since June 1998 until the present time at the height of 29 m. The eddy covariance system employed at the experimental site was similar to that used in the Euroflux project (Aubinet et al 2000). A complete description of the instrumentation and flux calculation is presented in Milyukova et al (2002) and Kurbatova et al (2008).

The temporal measurements of the tree stem, dead wood, and soil CO₂ emissions were performed during the growing seasons of 2002–2003 and 2007–2012. Wood respiration measurements were performed over 3–7-day periods on 3–4 spruce stems with representative diameters. One birch tree was also measured in 2003. The measurements were performed by an open-system method (see, e.g., Edwards and Sollins 1973) using different CO₂ analysers: ‘Kedr’ (Russia) in 2002–2007, LiCor-6262 in 2003, and LiCor-820

(LiCor Inc., USA) since 2008 (see details in Molchanov *et al* 2011a, 2011b). The CO₂ analyser readings were registered simultaneously with air and soil temperatures and air humidity. The radial growth of selected trees was also measured using band dendrometers. The respiration of dead wood was measured in August 2002 and 2003 on seven fallen trees and five dead standing trees using the same methods.

Soil CO₂ fluxes were measured by open and closed systems. In 2002, measurements were performed using the CO₂ analyser LI-6400 (LiCor, Inc., USA) with a standard soil chamber (closed system). In 2007–2008, soil respiration was measured in parallel with stem respiration using the same method (open system, Tatarinov *et al* 2011). Polyethylene transparent chambers with a projected area of 150–210 cm² were installed at the soil surface. The air was alternately pumped from the chamber and from the ambient air near the chamber inlet into the CO₂ analyser through a rotameter, and ejected into the atmosphere. The incoming air entered the chamber via inlets situated 3–4 cm above the soil surface. Preliminary experiments permitted us to choose a cross-sectional area of inlets that was sufficient to avoid the effect of underpressure in the chamber (Tatarinov *et al* 2009). Since 2009, soil respiration has been measured by different modifications of a closed system (Kurganova *et al* 2003, 2004) once every 7–10 days during the vegetation season at the same time of day (about 11 am). Measurements in 2009–2010 were performed using non-transparent cylindrical chambers without apertures placed at the soil surface. The air samples were taken from the chambers by a syringe at regular intervals and then analysed using the LiCor-820 (LiCor Inc., USA). A series of five simultaneous measurements was always performed. Since 2011, transparent chambers 40 × 40 × 40 cm³ have been applied the same way. The CO₂ analyser (SenseAir, type 074001, Sweden) and fan were mounted in the chamber and readings were made at regular intervals visually from the screen of the analyser. A pilot test showed that the open and closed (SenseAir) systems gave similar results: open system gave 70–130% of respiration measured by the closed one (103% in average), as the closed system applied in 2009–2010 gave about 60% of *R* measured by an open system or SenseAir closed system. Hence, the corresponding correction coefficient was applied for these measurements. In 2008 and 2011–2012, when applying transparent chambers, we measured the soil CO₂ balance (*B* = respiration – photosynthesis of mosses), whereas in 2002 and 2009–2010, when applying opaque chambers, we measured the respiration. In order to compare the results, in the latter case, the CO₂ balance was calculated by subtracting the mean photosynthesis of mosses (obtained by shading of transparent chambers and calculating the difference between CO₂ effluxes in shaded and unshaded chambers) from the measured *R*.

Statistical data processing was performed at two levels. (1) The dependence of *R* on the air temperature (*T*_{air}) and humidity was studied at the level of single measurements. In particular, the value of *Q*₁₀ was estimated from the exponential approximation $R = a \exp(bT_{\text{air}})$ as follows: $Q_{10} = \exp(10b)$ (Ryan 1990). (2) The seasonal course of respiration as well as its dependence on variables measured

with longer time intervals, such as tree diameter at breast height (DBH) or radial growth rate (for wood respiration), was evaluated at the level of respiration means per series of measurements. Up-scaling of the stem respiration of living trees was done as follows (Molchanov *et al* 2012). (1) The dependence of respiration per unit stem surface on *T*_{air} and tree DBH was derived for each measurement series in the form $R = (a + b * T_{\text{air}})^c \exp(c * \text{DBH})$. (2) The tree DBH distributions were obtained by measuring all trees with DBH ≥ 6 cm on a sample plot. (3) The dependence of tree height (*h*) on DBH was obtained for each species based on our measurements and data from the literature. It was then applied to calculate the stem surface for each DBH class. The stem respiration per hectare (*R*_{ha}) was calculated as follows:

$$R_{\text{ha}} = \sum_{\text{sp}} \sum_{\text{DBH}} (R_w(T_{\text{air}}, \text{DBH}, \text{sp})) s(\text{DBH}) n(\text{DBH}, \text{sp}),$$

where *R*_w is the respiration per unit stem surface, sp is species, *s* is the stem surface of one tree, and *n* is the stocking density per hectare.

Because for dead standing trees the respiration changed significantly with diameter, a modified calculation procedure was applied for them. The respiration of one stem was calculated by integrating the respiration per unit area along the stem:

$$R = \int_0^H r(T_{\text{air}}, D(h), \text{sp}) \pi D(h) dh.$$

Detailed data on fallen stem distributions were not available. Consequently, for its respiration we up-scaled data from the literature on the distribution of coarse woody debris according to the stage of decomposition in a similar forest type (Storozhenko 2002). First we derived the dependence of the mean (per series) respiration of a fallen stem on its stage of decomposition and then the obtained data was multiplied by the corresponding storages and summarized.

Since respiration of living stems were not measured in August 2002 (dry season), the data from August 2003 (wet season) was applied, multiplied by a correction coefficient obtained by comparison of the data for August 2008 (wet season) and 2010 (dry season) for the same trees.

Daily totals of CO₂ efflux from soil were calculated based on observed daily averages (detailed description in Kurganova *et al* 2003). The uncertainty of soil respiration includes spatial and temporal variability. The spatial variability of soil respiration was evaluated on the basis of 2002 and 2010–2011 data when *R* was measured at 5–7 points simultaneously. The diurnal variability of *R* was evaluated based on continuous 24 h measurements in 2008. The total (spatial and temporal) variability of *R* was calculated by combining the temporal variability from 2008 with the spatial variability from 2002 and 2010–2011.

3. Results

3.1. Weather conditions in the measurement period

The weather conditions in the measuring periods were characterized by high variability. Vegetation seasons 2002 and

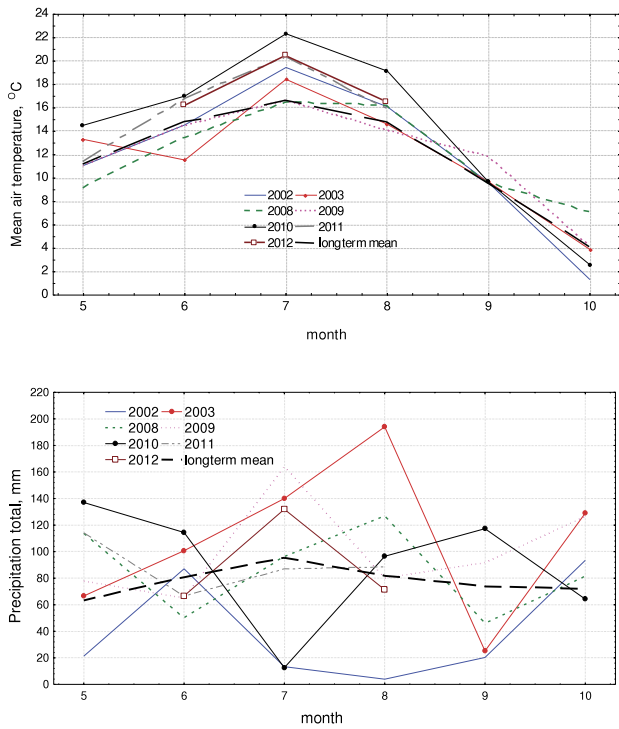


Figure 1. Monthly average air temperature (upper figure) and monthly precipitation during vegetation seasons under study (lower figure). Long-term mean values were derived from meteorological observations in the CFSNBR from 1970 to 2010.

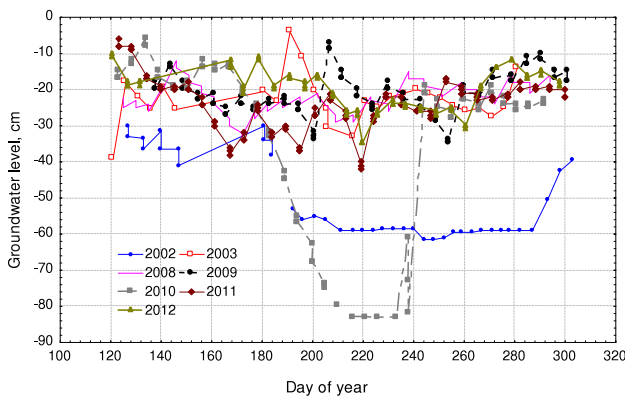


Figure 2. Ground water level during the vegetation seasons under study.

2010 were extremely warm and dry (figures 1 and 2). In particular, in 2010 there was only 21.3 mm of precipitation between 17 June and 20 August. In contrast, the season 2003 was very wet, especially July and August, and no periods without precipitation longer than nine days occurred during the summer time. The seasons of 2008–2009 and 2011–2012 were close to climatic means. The groundwater levels in 2002 and 2010 were affected by strong droughts (figure 2).

3.2. Soil respiration

Results of measurements of CO₂ emission from the soil surface with vegetation cover (*R*) are shown in figures 3

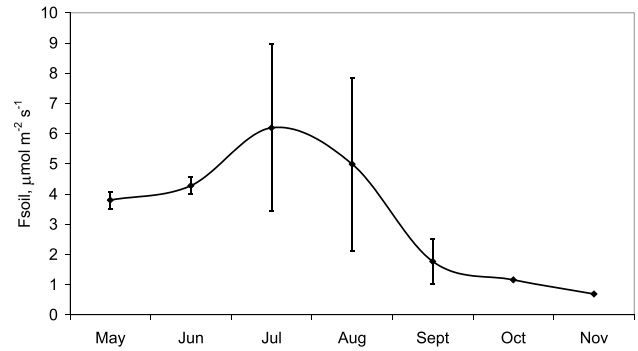


Figure 3. Average seasonal course of the CO₂ emission rate in the paludified shallow-peat spruce forest for seasons 2002–2003 and 2007–2012. The vertical lines represent ±1 standard deviation.

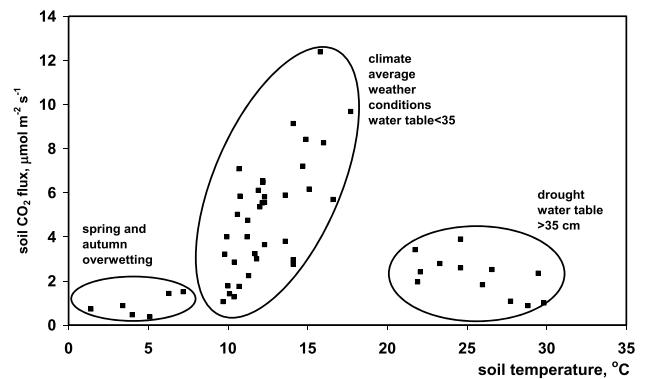


Figure 4. Relationship between soil temperature and soil respiration for different groundwater levels.

and 4. We found that the soil fluxes were characterized by high seasonal variability—from 0.7 to 10 μmol m⁻² s⁻¹. Maximum *R* was observed in July and the first part of August. Minimal fluxes were found in October and November. Generally, the seasonal course of *R* depended on the soil temperature and ground water level. Figure 5 shows the dependence of CO₂ emission on the soil temperature for different groundwater levels. It is necessary to notice that, under high drought conditions, when the groundwater level fell below 35 cm, the soil respiration was low and did not depend on the temperature. Maximum respiration occurred under moderate moisture conditions and soil temperature (15–20 °C).

Periods of over-watering were usually observed in the conditions of low soil temperature, so it was difficult to determine the separate effect of over-watering on soil fluxes based on our field measurements.

3.3. Wood respiration

Generally, the stem respiration of spruce increased rapidly in May, maintained high levels from June to the end of September, and fell rapidly in October (table 1). Means of *R_w* per tree and per series of measurements in midsummer were about 3–5 μmol m⁻² s⁻¹ for dominant trees (up to 7 μmol m⁻² s⁻¹ in June 2003) and about 1–2 μmol m⁻² s⁻¹ for subdominant trees (see table 1).

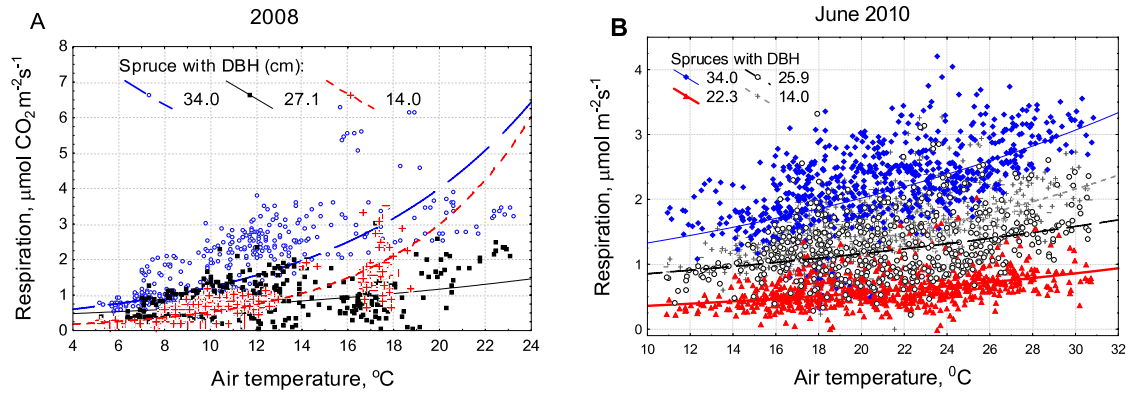


Figure 5. Examples of temperature dependences of stem respiration (exponential approximation). The tree with DBH 22.3 cm at the end of season 2010 had a marked defoliation.

Table 1. Mean (per sample tree and per measurement series) tree stem respiration.

Tree	Sample trees							
	S16	S6	S18	S2	S4	S3	B	
Species	Spruce	Spruce	Spruce	Spruce	Spruce	Spruce	Birch	
DBH ^a (cm)	14.0	22.3	34.0	27.1	25.9	21.0	29.4	
Tree class ^b	IV	III	I	II	II	III	I	
Period	Mean air temp. (°C) ^c	Mean CO ₂ efflux (µmol m ⁻² s ⁻¹) (± standard error)						
03–09.08.02	17.9	0.15 (±0.01)						
4–8.06.03	16.5	1.54 (±0.24) 7.41 (±0.68) 4.65 (±0.35)						
29.07–05.08.03	20.5	2.19 (±0.24)	1.67 (±0.58)	6.66 (±0.44)	1.03 (±0.07)			
10–17.09.03	13.5	1.41 (±0.17)	0.83 (±0.16)	4.49 (±0.57)	0.67 (±0.05)			
16–22.10.03	–1.3	0.86 (±0.23) 0.17 (±0.04)						
29.06–02.07.07	13.0	5.66 (±0.60) 1.56 (±0.13)						
23–29.09.07	7.1	1.15 (±0.13)	0.86 (±0.09)					
19–22.05.08	10.5	0.80 (±0.03)	0.88 (±0.02) 0.74 (±0.01)					
30.07–03.08.08	13.3	1.09 (±0.04)	2.58 (±0.05) 1.87 (±0.02)					
05–13.09.08	11.0	0.67 (±0.04)	1.14 (±0.10) 0.91 (±0.08)					
16–19.05.09	7.1	0.54 (±0.02)	0.17 (±0.01)					
14.06.10	18.5	1.17 (±0.05)	0.68 (±0.10)	1.78 (±0.04)	0.70 (±0.05)	1.04 (±0.13)		
19–26.06.10	22.2	1.68 (±0.02)	0.73 (±0.01)	2.47 (±0.03)	1.41 (±0.09)	2.07 (±0.05)		
27.06–2.07.10	19.8	1.40 (±0.02)	0.51 (±0.01)	2.07 (±0.02)	0.52 (±0.03)	1.11 (±0.02)		
05–10.08.10	34.0	1.71 (±0.15)	1.00 (±0.08)	2.57 (±0.22)	1.71 (±0.12)	1.38 (±0.15)		
22–23.08.10	16.5	0.66 (±0.04)	1.03 (±0.09) 0.61 (±0.02) 1.22 (±0.07) 0.32 (±0.06)					
03.09.10	10.8	0.40 (±0.04)	0.26 (±0.01) 0.56 (±0.04) 0.99 (±0.06)					

^a DBH values correspond to the first year of measurements.

^b Tree class (according to craft) characterizes tree position in the stand from I (dominants) to V (suppressed).

^c Air temperature was averaged within the time of measurements.

The positive dependence of R_w (per unit stem surface) on the tree DBH was generally nonlinear with relatively high respiration of smaller trees. R_w was practically independent of the DBH for DBH < 30 cm, and it was considerably higher only for the biggest sample tree. When considering respiration per unit stem volume (R_v), for smaller trees it was similar or even higher (in midsummer) than R_v of bigger trees.

The increasing dependence of R_w on air temperature was observed for all measuring periods and for most of the trees (figure 5), but its determination coefficient was relatively low and usually did not exceed 0.5. In some cases temperature dependence was missing for small or damaged trees. Often it was close to linear within the range of temperatures observed. The values of Q_{10} obtained varied considerably between trees and seasons, being generally higher for bigger trees and for moister seasons. Thus, during the wet season 2003, Q_{10} ranged from 2.0 to 2.5, under moderate conditions (2008) it ranged from 1.4 to 4.1 (mean value 2.4), and under drought stress it reached 1.9 in 2002 and from 1.3 to 1.6 in 2010. A weak but significant negative correlation of R_w with air humidity was also observed for most of the sample trees, in particular under drought stress (2010). This illustrates the result, obtained at the level of respiration means, that the respiration did not decrease during severe drought stress, but it decreased after the end of the drought due to the decrease of temperature (see table 1). In 2003 and 2008, R_w strongly ($r = 0.80$) correlated with the gross primary production shifted three days later at the daily level. In 2010, the correlation was poor, which corresponds to the statement above.

The diurnal amplitude of R_w in May was relatively low. From June to August, the diurnal minimum and maximum R_w were observed in the morning at around 5–8 h and in the evening at around 18 h, respectively. In September, the diurnal minimum of R_w shifted to noon.

The stem respiration in the forest in this study was generally lower than the respiration of trees of similar positions in the canopy (tree class) in the more dry forest in the same study area when expressed per unit stem surface, but slightly higher when expressed per unit stem volume (Tatarinov et al 2010).

The increasing dependence of stem respiration on stem cross-section growth rate (ds/dt) was observed under favourable weather conditions (figure 6; see Molchanov et al 2011b). The opposite situation was observed in 2010 under drought stress. In this case the dependence $R(ds/dt)$ was slightly negative, which can be explained by the masking of the true growth by high shrinkage during the drought and swelling after its end.

The respiration of dead wood ranged from 0.1 to $5.9 \mu\text{mol m}^{-2} \text{s}^{-1}$ for dead standing trees and from 0.1 to $12.5 \mu\text{mol m}^{-2} \text{s}^{-1}$ for fallen trees, with means of 1.8 and $1.0 \mu\text{mol m}^{-2} \text{s}^{-1}$, respectively (Molchanov et al 2011a). It depended significantly on the presence of bark (R_w was much higher for wood with bark) and the stage of decomposition (being the highest for medium decomposition). High positive dependence close to exponential was observed also for wood moisture. The effect of temperature was less pronounced. The seasonal course of dead wood respiration reached its maximum in September.

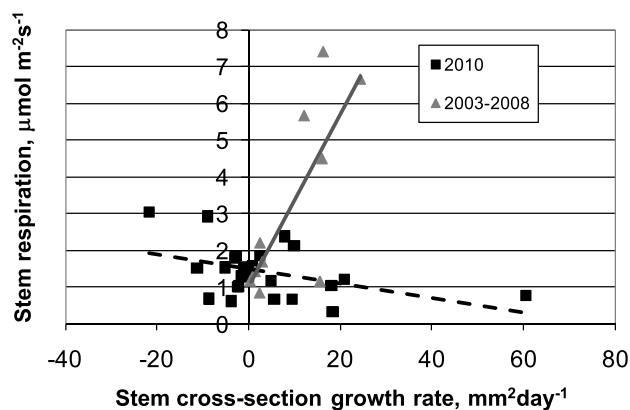


Figure 6. The dependence of stem respiration on stem radial growth. Each point corresponds to one tree and a series of measurements.

The partitioning of the ecosystem respiration is shown on table 2.

4. General discussion and conclusions

Eddy covariance-based estimates of net ecosystem exchange have been made for 14 sites in Russia (Dolman et al 2012). Three clusters of sites were selected: a wetland cluster, where the annual CO_2 land to atmosphere fluxes that occur are between -50 and $-90 \text{ g C m}^{-2} \text{ yr}^{-1}$, a grassland cluster, with fluxes between -125 and $-170 \text{ g C m}^{-2} \text{ yr}^{-1}$, and a forest cluster with more variable net ecosystem exchange (NEE) rates. Among seven forest sites, four sites show an uptake between -200 and $-300 \text{ g C m}^{-2} \text{ yr}^{-1}$, and the three others have an NEE between 0 and $-150 \text{ g C m}^{-2} \text{ yr}^{-1}$. All forest sites appear to be net sinks of CO_2 , as expected for growing forests. The paludified shallow-peat spruce forest in the southern taiga of European Russia is the only site that is on average a source of CO_2 to the atmosphere. Generally this can be explained by large respiration, which is higher from the boggy soil.

Previous research conducted in the CFSNBR (Minayeva et al 2008, Šantrůčková et al 2010) showed that carbon stocks in mineral soils are many times smaller than in waterlogged shallow-peat soils and an order of magnitude smaller than in peat bog soils. The carbon stored in the sward podzolic soils in mixed spruce forests is not higher than $2\text{--}4 \text{ kg C m}^{-2}$. The white podzolic peaty soils under spruce forests contain up to 6 kg C m^{-2} . In wetter forest with paludified shallow-peat soils, the carbon storage increases to 50 kg C m^{-2} , while the storage in peat bog and fens is about 100 kg C m^{-2} . So shallow-peat soils are a significant pool of carbon in comparison with well-drained podzolic soils.

Our research confirmed that the carbon budget of the site under study depends significantly on the soil respiration. The soil respiration ranged from 20 to 67% of the total respiration (49% on average), which is within the range reported by other authors (Wang et al 2004, Hamilton et al 2002, Law et al 1999, Lavigne et al 1997, Goulden et al 1996, Kurganova et al 2010, Kurganova and Kudeyarov 2012). The long-term

Table 2. Monthly sums of soil, stem, and ecosystem respiration ($\text{mol m}^{-2} \text{ month}^{-1}$; \pm standard error, % of ecosystem respiration in parentheses), average air temperature, precipitation total in the spruce paludified spruce forest.

Observation period	Mean air temp. (°C)	Precip. (mm)	Soil respiration	Live stem respiration	Dead stem respiration	Ecosystem respiration
2002–Aug	16.1	3.9		4.6(36%)	0.8(6%)	12.9 \pm 1.4
2003–Jun	11.5	100.7	9.5(52%)	5.5(30%)	1.6(9%)	18.1 \pm 0.9
2003–Jul	18.4	140.0	11.9(42%)	4.5(16%)	1.2(4%)	28.1 \pm 0.9
2003–Aug	14.6	194.0	11.9(57%)	4.5(21%)	1.2(5%)	21.0 \pm 1.0
2003–Sept	9.7	25.2	10.4(60%)	3.1(18%)	0.8(6%)	17.5 \pm 0.9
2003–Oct	3.9	129.0	3.1(39%)	0.3(4%)	0.1(1%)	8.0 \pm 0.9
2008–May	9.1	113.8	9.0 \pm 0.7(60%)	1.3(10%)		13.7 \pm 0.6
2008–Aug	16.2	127.0	11.2 \pm 0.4(57%)	3.2(14%)		23.0 \pm 1.0
2008–Sep	9.5	46.2	8.7 \pm 0.6(58%)	1.5(10%)		14.9 \pm 0.9
2009–Jun	14.5	65.2	10.4 \pm 0.8(41%)			25.0 \pm 0.9
2009–July	16.6	164.0	14.5 \pm 1.2(51%)			28.3 \pm 0.1.0
2010–Jun	17.0	114.4		7.4(39.4)		18.8 \pm 0.7
2010–July	22.3	12.6	8.1 \pm 0.7(35%)	1.4(6%)		23.4 \pm 0.9
2010–Aug	19.1	96.5	6.2 \pm 0.4(35%)	2.6(15%)		17.6 \pm 0.8
2010–Sept	9.7	117.3	3.2 \pm 0.6(22%)	1.0(7%)		14.4 \pm 0.8
2011–Jun	16.7	66.6	11.7 \pm 1.6(49%)			23.8
2011–Jul	20.3	87.1	19.2 \pm 1.1(67%)			28.9
2011–Aug	15.9	88.5	10.4 \pm 1.2(42%)			24.6
2011–Sep			7.3 \pm 1.0(48%)			15.3
2011–Oct		41.5	3.1 \pm 0.5(43%)			7.2
2011–Nov			1.8 \pm 0.4(44%)			4.1
2012–Jun	16.1	66.7		11.9		
2012–Jul	20.4	131.9	24.4			
2012–Aug	16.5	71.3	16.9			

ecosystem water balance (particularly the depth of the water table) is clearly important, and may explain most of the observed interseasonal and interannual variability of soil carbon flux. In the dry season of 2010, its portion was much smaller than in other seasons, ranging from 22 to 35%. Our observations showed that the soil respiration was the highest for a moderately deep groundwater level (2002), whereas under severe drought (2010) or over-watering it was smaller. The reason may be the following. Under a high water level the peat decomposition is inhibited by flooding of peat by water and its low pH. In turn, under a low water level the peat decomposition is limited by insufficient peat moisture. Under a moderate water level an optimum is reached between these two factors. Similar results were obtained by Mäkiranta *et al* (2008) in Finland. The seasonal and interannual variability of soil respiration fluxes obtained in the paludified forest is comparable with results of other studies in wetlands. Observations in different peatlands show considerable variability in the relationship between water level and measured soil CO₂ emissions (Silvola *et al* 1996, Lafleur *et al* 2005). Studies have further shown that lowering the water level within sites increases the CO₂ emissions only to a certain depth (Silvola *et al* 1996, Chimner and Cooper 2003), and that the water level may in some cases even sink to a depth at which some researchers have suggested that drying of the peat surface may limit the decomposition rate of organic matter (Liefers 1988, Laiho *et al* 2004).

It is interesting to notice that the soil respiration in the drier complex spruce forest situated about 2 km from the sample plot had much lower interannual variation, being similar to *R* in our stand under normal conditions and smaller under moderate drought conditions (Tatarinov *et al* 2011).

The values of respiration of living stems obtained in the present study were comparable to the results of other studies obtained for Norway spruce. Tselniker and Malkina (1993) obtained values of the stem respiration of 25-year-old spruce trees in summer in the Moscow region of Russia that were about 0.04–0.2 mg CO₂ m⁻² s⁻¹ (i.e., from 0.9 to 4.6 $\mu\text{mol m}^{-2} \text{ s}^{-1}$), which correspond well with our results. Values of stem respiration of 14-year-old Norway spruce in Moravia in July observed by Acosta *et al* (2010) ranging from 2.5 to 4 $\mu\text{mol m}^{-2} \text{ s}^{-1}$ fall within the same span. The results of the same authors for 22-year-old spruce trees were slightly higher, ranging from 0.34 to 6.52 $\mu\text{mol m}^{-2} \text{ s}^{-1}$ (Acosta *et al* 2008). The respiration of living stems was about 10–20% of the total respiration, which also corresponds to the reports of other authors (Shibistova *et al* 2002, Wang *et al* 2004, etc).

Dead wood respiration was rather small compared to that of the dry spruce forest studied by Molchanov *et al* (2011a) for two reasons. (1) The stand under study is very stable, in contrast with a more dry stand, which sometimes experienced mass dying of spruce and windfalls (the last one was just in 2002). Consequently there is rather little coarse woody debris in the paludified forest. (2) The wood in the paludified forest has a higher density than in the dry spruce forest due to the low growth rate, and hence its decomposition is slower.

We conclude that the carbon budget of a boreal paludified forest is strongly dependent on the soil CO₂ emission. Climate warming will considerably increase the respiration only if the resultant decrease in moisture content of the upper peat layers is minor and, thus, conditions remain optimal for the decomposition of organic matter.

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