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## Article

# Clear-cutting effects on components of the carbon balance in a bilberry-type pine forest in southern Karelia

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**Abstract.** Photosynthetic carbon flux and soil respiration are major determinants of the carbon balance of terrestrial ecosystems. Components of the carbon exchange of woody plants and soils were estimated in a 10-year-old clear-cut site of mid-boreal bilberry-type pine forest in southern Karelia during the warm season (July–August) in 2017–2019. The control was trees of the same age (10–15 years) and natural soils under the canopy of a mature bilberry pine forest. A comparison of the parameters of CO<sub>2</sub> gas exchange in Scots pine (*Pinus sylvestris* L.), silver birch (*Betula pendula* Roth), gray alder (*Alnus incana* (L.) Moench), and aspen (*Populus tremula* L.) revealed that photosynthetic uptake of CO<sub>2</sub> exceeded its release by foliage during dark respiration in all the species more significantly in the regenerating clear-cutting (6–10-fold) than under mature stand canopy (3–6-fold). The rate of photosynthesis in trees of the same age was higher in deciduous species compared to pine both in the clear-cut site (16.6–17.6 and 7.4 μmol/m<sup>2</sup>·s) and under pine forest canopy (11.2–12.3 and 5.5 μmol/m<sup>2</sup>·s). The contributions of soil emission to the atmospheric CO<sub>2</sub> flux in the regenerating clear-cutting (4.6 μmol/m<sup>2</sup> s) and under the stand canopy (5.9 μmol/m<sup>2</sup>·s) are reported. Intra-seasonal variability of the parameters of carbon exchange in woody plants and soil was high as opposed to the relatively low variation among years in both sample plots.

**Keywords:** logging, natural forest regeneration, CO<sub>2</sub> gas exchange in woody plants, CO<sub>2</sub> emission from soil surface, podzolic sandy soils, environmental factors, middle taiga

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**Научная статья****Влияние сплошной рубки на составляющие углеродного баланса сосняка черничного Южной Карелии**В.Б. Придача\* , Д.Е. Семин*Институт леса Карельского научного центра РАН, 185910, Россия, Республика Карелия, г. Петрозаводск, ул. Пушкинская, д. 11*

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**Аннотация.** Поглощение растениями  $\text{CO}_2$  из атмосферы в процессе фотосинтеза и дыхание почвы в наибольшей степени определяют углеродный баланс наземных экосистем. На основе 3-летних наблюдений в теплый период года (июль–август 2017–2019 гг.) проведена оценка составляющих углеродного обмена древесных растений и почвенного покрова на сплошной вырубке 10-летней давности среднетаежного сосняка черничного в условиях Южной Карелии. Контролем послужили одновозрастные деревья (10–15 лет) и естественные почвы под пологом спелого сосняка черничного. Сопоставление показателей  $\text{CO}_2$ -газообмена сосны обыкновенной (*Pinus sylvestris* L.), березы повислой (*Betula pendula* Roth), ольхи серой (*Alnus incana* (L.) Moench) и осины (*Populus tremula* L.) выявило в условиях сплошной рубки более интенсивное связывание  $\text{CO}_2$  в процессе фотосинтеза относительно его выделения листом при темновом дыхании у всех видов (в 6–10 раз) по сравнению с таковыми у деревьев под пологом спелого древостоя (в 3–6 раз). Наибольшая интенсивность фотосинтеза для одновозрастных деревьев отмечена у лиственных видов относительно сосны как в антропогенно трансформированном биоценозе (16.6–17.6 и 7.4 мкмоль/м<sup>2</sup> с), так и под пологом сосняка черничного (11.2–12.3 и 5.5 мкмоль/м<sup>2</sup> с). Показан вклад почвенной эмиссии в атмосферный поток  $\text{CO}_2$  на сплошной вырубке (4.6 мкмоль/м<sup>2</sup> с) и под пологом древостоя (5.9 мкмоль/м<sup>2</sup> с). Отмечено преобладание внутрисезонной вариативности на фоне схожих среднесуточных величин показателей углеродного обмена древесных растений и почвы на обоих экспериментальных участках.

**Ключевые слова:** рубки леса, естественное возобновление,  $\text{CO}_2$ -газообмен древесных растений, эмиссия  $\text{CO}_2$  с поверхности почвы, подзолистые песчаные почвы, факторы внешней среды, средняя тайга

**Финансирование.** Финансовое обеспечение исследований осуществлялось из средств федерального бюджета на выполнение государственного задания КарНЦ РАН (Институт леса КарНЦ РАН) и при финансовой поддержке РФФИ (грант № 17-04-01087-а). Исследования выполнены на научном оборудовании Центра коллективного пользования Федерального исследовательского центра «Карельский научный центр Российской академии наук».

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## Introduction

Boreal forests are among the key regulators of our planet's climate through matter and energy exchange (Bonan, 2008; Groisman et al., 2017). They store immense amounts of biogenic carbon, comparable to the carbon stock of tropical forests. The current global warming (IPCC, 2013), triggered by air temperature rise, changes in atmospheric gas composition and land surface moisture conditions, can influence the dynamics and rates of biophysical and biochemical processes in plants (Lukac et al., 2010; Niinemets, 2010; Olchev et al., 2013; Price et al., 2013; Sazonova et al., 2019) and in soil (Karelin et al., 2020; Kurganova et al., 2020; Luo and Zhou, 2010; Mukhortova et al., 2021; Wiesmeier et al., 2019). Natural ecosystems are also significantly affected by human impacts, such as pollution of air and soil water, land use changes, or logging (Groisman et al., 2017; Pridacha et al., 2011; Shorohova et al., 2019). To wit, international estimates of the total forest area (FAO, 2020) show that 420 million hectares of forest have been lost globally due to logging since 1990. However, global deforestation has lately (2010–2018) slowed down by 30% (to 8 mln ha per year) versus 2000–2010 (FAO, 2020).

Russian forests constitute one-fifth of global forest resources, including over a half of the planet's boreal forests (FAO, 2020). According to the latest inventory, forests in the Russian Federation are 98.4% made up of natural stands (Filipchuk et al., 2022). Meanwhile, the area of mature and over-mature pine stands in the north-west of the boreal zone of European Russia, in particular in the Republic of Karelia, has declined over the past 60 years (1956–2014) by 51% as a result of large-scale clear-cutting, while the share of deciduous stands has increased (Ananyev and Moshnikov, 2016). Conifer-dominated stands currently account for 87.5% of the forested area in Karelia, including 64.3% of pine-dominated and 23.2% of spruce-dominated stands<sup>1</sup>.

Logging substantially alters the forest cover and forest soils (Dymov, 2017; Keeman and Kimmins, 1993; Williams et al., 2014), the microclimate, and the water regime of soils, entailing a rapid loss of carbon from the forest ecosystems (Mamkin et al., 2019; Olchev et al., 2017). In this context, some authors report that retention of advance regeneration when logging forests in the European North can ensure 1.5–2-fold higher photosynthetic fixation of CO<sub>2</sub> by young trees in cut-over sites owing to the photosynthetic apparatus adapting to higher illumination upon forest canopy removal (Konovalov and Zarubina, 2019; Tuzhilkina, 2022). At the same time, soil respiration in a recently harvested forest site was shown to depend on the degree of topsoil disturbance, the presence of tree litter and logging residues on the surface (Molchanov et al., 2017). Prevalence of carbon losses to respiration over its photosynthetic fixation can alter the functional role of the terrestrial ecosystem, converting it from a sink to a source of atmospheric carbon (Bobkova and Kuznetsov, 2022; Fatichi et al., 2019; Olchev et al., 2017; Schulze et al., 1999; Valentini et al., 2000). A comprehensive investigation of CO<sub>2</sub> emission and uptake by a natural ecosystem requires finding the contributions of its individual components to the CO<sub>2</sub> balance. With this in mind, we made it our aim to comparatively estimate the components of the carbon exchange of trees and soils in a clear-cut bilberry-type pine forest site and under the forest canopy in the middle-taiga subzone of Karelia during three growing seasons.

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<sup>1</sup> State Report on the Environment in the Republic of Karelia in 2020, 2021.

## Material and methods

### **Characteristics of the climate, vegetation, and soils**

The study was carried out in the middle taiga subzone of North European Russia, in the Kondopoga District, Republic of Karelia, in July and August 2017–2019. The climate in the study area is of the sub-arctic type according to the Köppen classification (Peel et al., 2007), with substantial amounts of precipitation during a year (550–750 mm, including 350–400 mm in the period from May through October) and high relative air humidity (75% on average) (Nazarova, 2021). Mean annual air temperature is +3.6 °C; mean monthly temperatures range from +17.1 °C (July) to –8.4 °C (January) (data covering 1991–2020) (Nazarova, 2021). Mean air temperature over the growing season (May–September) is +13 °C. The total radiation balance over the growing season is 1130 MJ/m<sup>2</sup>. According to data from the Kondopoga weather station<sup>2</sup>, the temperature regime in the study area in the period from May through September 2017–2019 featured an alternation ( $1.2 \leq \Delta T_{\text{seas}} \leq 1.8$ ) of warmer (2018) and colder seasons (2017 and 2019). In 2017–2019, from May through September, the precipitation regime was characterized by an alternation of rainy (349 mm) and drier periods (245 mm): precipitation deficit relative to the normal multi-decadal level was observed in May–June 2017 and 2018 (80–88 and 44–52% of the normal, respectively) and in June 2019 (46% of the normal).

Surveys were done in sample plots (SPs) established in a bilberry pine forest site clear-cut in 2009 (Pridacha et al., 2021) (SP 1) and in the natural environment of a 95-year-old bilberry pine stand (SP 2) (Fig. 1). Clear-cutting of the stand was done in summer, in 12 ha area, in a mechanized manner. The distance between the SPs is less than 1 km. The sites SP 1 (10×20 m) and SP 2 were selected so as to have homogeneous relief, parent rock, and soil hydrological regime (30×50 m) (Table 1).

The young stand formed through natural regeneration in the clear-cut site is made up of regenerating Scots pine *Pinus sylvestris* L. (70%) mixed with silver birch *Betula pendula* Roth (30%) and some aspen *Populus tremula* L. The understory comprises gray alder *Alnus incana* (L.) Moench, willow *Salix* sp., rowan *Sorbus aucuparia* L. The dominants in the ground cover are *Chamaenerion angustifolium* (20%), *Rubus saxatilis* (10%), *Calamagrostis arundinacea* (10%), *Avenella flexuosa* (3%). The moss-lichen layer is poorly developed, represented by occasional patches of mosses *Dicranum* sp. and *Polytrichum juniperinum* Hedw. The soil is an Arenic Albic Podzol (Shishov et al., 2004). The bulk of roots are concentrated within 2–25 cm depth. The groundwater table depth is 1.2 m.

The mature bilberry-type pine stand is dominated by *P. sylvestris* (90%) mixed with *B. pendula* (10%). The stand of quality class I has a relative stocking density of 0.6 and 304 m<sup>3</sup>/ha timber volume. Advance-regeneration *P. sylvestris*, *B. pendula* and *P. tremula* are mostly present in the parent stand canopy gaps. The understory is made up of *A. incana*, with singular *S. aucuparia* and juniper *Juniperus communis* L plants. The ground cover dominants are the subshrubs *Vaccinium myrtillus* (30%), *Melampyrum pratense* (3%) and *Vaccinium vitis-idaea* (3%), and the mosses *Pleurozium schreberi* (60%) and *Hylocomium splendens* (4%). The soil is an Arenic Albic Podzol (Shishov et al., 2004). The bulk of roots are concentrated within 2–25 cm. The groundwater table depth is 1.2 m.

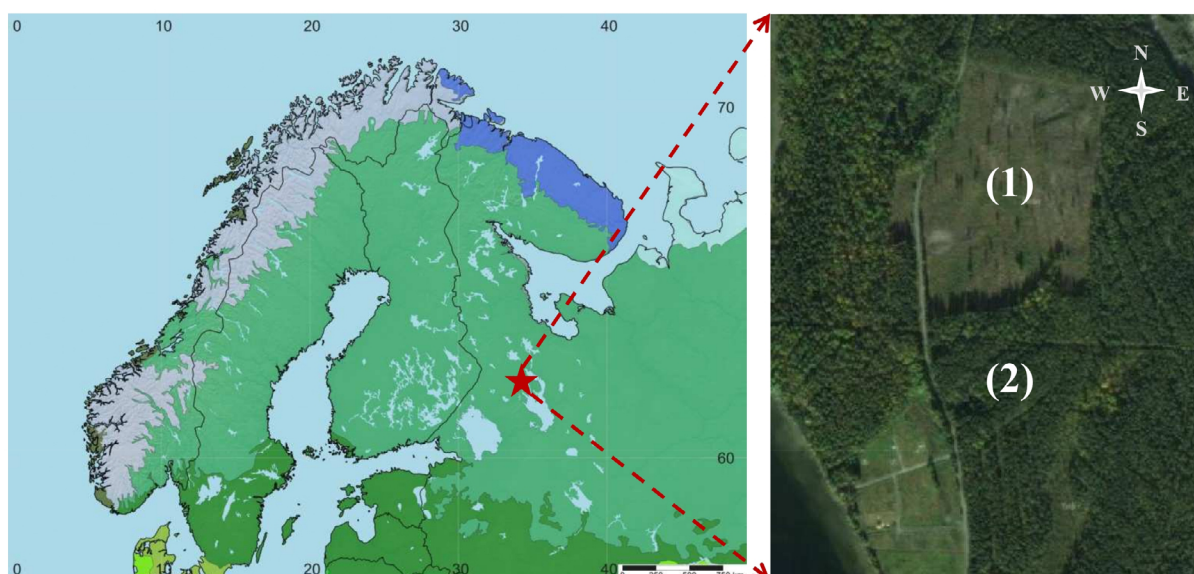
Surveys in the clear-cut site and the pine stand included a complete tree count (at least 150 young-generation pine, birch, aspen, and alder trees in each SP), measurements of the trunk diameter (at 1.3 m height) and height of all the trees at 0.01 and 0.1 m accuracy, respectively. Based on these measurements, model trees with the following average height and diameter parameters were selected: not exceeding 4.5 and 3.7 m, 4.3 and 2.9 cm in the clear-cut site and the pine stand, respectively. The young stand composition was derived from the number of trees of different species by enumerating small (up to 0.5 m high), medium (0.51–1.5 m), and large (taller than 1.5 m) regeneration (understory) plants following a procedure commonly accepted in Russia (Osnovy lesnoi taksatsii..., 2021). A more detailed description of the vegetation and soils of both SPs can be found in our previous paper (Pridacha et al., 2021).

### **Indices of CO<sub>2</sub> exchange in plants**

Field data on the leaf gas exchange were obtained for an even-aged young stand (10–15 years old) of Scots pine, silver birch, gray alder, and aspen growing in a clear-cut site and under the canopy of a mature bilberry-type pine stand. The study sites were selected in view of the distribution of Karelian forests by the prevalent tree species<sup>3</sup>.

<sup>2</sup> Weather schedule. Web page. URL: <https://rp5.ru/> (accessed: 16.04.2024).

<sup>3</sup> State Report on the Environment in the Republic of Karelia in 2020, 2021.



**Fig. 1.** Locations (red asterisks) of the clear-cut site (1) and the bilberry-type pine stand (2) in the study area.

The rates of leaf photosynthesis ( $A$ ,  $\mu\text{mol}/\text{m}^2\cdot\text{s}$ ) and dark respiration ( $R_d$ ,  $\mu\text{mol}/\text{m}^2\cdot\text{s}$ ) in birch, alder, and aspen and in one-year-old pine needles in the clear-cut site and under pine forest canopy were measured in July 2017–2019 during daytime, from 10:00 a.m. to 04:00 p.m., in undetached mid-crown leaves using portable photosynthesis system LI-6400XT (LI-COR Inc., USA). The measurements were always done on fully formed leaves without visible damage, following a standard protocol (Pridacha et al., 2021) in a standard leaf chamber illuminated by LI-6400-02BLED (LI-COR Inc., USA) at 1600 or 0  $\mu\text{mol}/\text{m}^2\cdot\text{s}$  to measure the rates of photosynthesis and dark respiration, respectively, at  $\text{CO}_2$  concentration of 400  $\mu\text{mol}/\text{mol}$ , air temperature of 23 °C, and air flow rate of 400  $\mu\text{mol}/\text{s}$ . Leaf  $\text{CO}_2$  gas exchange measurements were taken in three replications for each tree and in 5 replications for each species in both SPs five times a month. The average duration of leaf accommodation to the leaf chamber was 15 minutes. To avoid stomatal closure during measurements, relative air humidity in the measuring chamber was kept within 50–70% (Busch, 2018).

Meteorological measurements in each SP were done using automated temperature and relative humidity loggers TRV-2 (Engineering Technologies, Russia). The rate of incident photosynthetically active radiation (PAR) in each SP was measured using LI-6400XT system (LI-COR Inc., USA).

### **Soil respiration**

The  $\text{CO}_2$  flux from soil surface in the clear-cut site and the bilberry pine forest site was studied in the last third of July – first third of August of 2017–2019 from 12:00 to 16:00 h on clear days without rainfall (Metody issledovaniia..., 2005). The measurements were done by a closed (opaque) chamber method using portable infrared gas analyzer LI-8100A (LI-COR Inc., USA) fitted with sensors of soil temperature (Omega, USA) and volumetric water content ECH<sub>2</sub>O EC-5 (Decagon Devices Inc., USA). To prepare for the measurements, PVC rings of 20 cm in diameter and 12 cm high were pressed down into the ground to 6 cm depth in both the clear-cut site and in the pine stand, without removing the ground vegetation, 3 hours before the start of observations. The total volume of the measurement system was 6749.8 cm<sup>3</sup>, including 4843 cm<sup>3</sup> of the LI-8100-103 survey chamber (LI-COR Inc., USA) and 1906.8 cm<sup>3</sup> of the ring (based on the distance from the soil surface to the top of the ring)<sup>4</sup>. Emission from soil in cutting blocks and skid trails of the clear-cut site was estimated with a differentiation into three ground vegetation microgroups (herbaceous – SP 1<sub>1</sub>, true-moss – SP 1<sub>2</sub>, fine woody debris – SP 1<sub>3</sub>). All in all, 12 rings were deployed: 3 in the clear-cut site (three in each of SP 1<sub>1</sub>, SP 1<sub>2</sub>, SP 1<sub>3</sub>) and 3 in the bilberry pine stand (SP 2, bilberry-true moss microgroup). In all the sites, rings were positioned between tree crowns,

<sup>4</sup> LI-8100A, 2012. Automated soil  $\text{CO}_2$  flux system. LI-8150 Multiplexer. Instruction manual.

**Table 1.** Microclimatic and soil conditions in the clear-cut bilberry pine forest site and under undisturbed bilberry pine forest canopy in July 2017–2019 (daytime mean  $\pm$  standard error). PAR – photosynthetically active radiation;  $CO_{2air}$  –  $CO_2$  concentration in the surface air;  $T_{air}$  – air temperature; VPD – water vapor pressure deficit;  $T_{soil}$  – soil temperature (0–20 cm layer); VWC – volumetric water content (0–20 cm layer);  $C_{tot1}$  – total carbon content in the top organic horizon of soil (0–3/0–4 cm);  $C_{tot2}$  – total carbon content in the soil mineral horizon (3–24/4–27 cm);  $N_{tot1}$  – total nitrogen content in the top organic horizon of soil (0–3/0–4 cm);  $N_{tot2}$  – total nitrogen content in the soil mineral horizon (3–24/4–27 cm);  $pH_{KCl}$  – salt-displaceable acidity. Letter indexes indicate significantly different means for the clear-cut site and the bilberry pine forest ( $p < 0.05$ ).

Parameter	Clear-cut site	Bilberry pine stand
Coordinates	N 62°10'28.1" E 33°59'58.8"	N 62°10'10.8" E 34°00'05.4"
PAR, $\mu mol \cdot m^{-2} \cdot s^{-1}$	1216.8 $\pm$ 23.4 <sup>a</sup>	239.2 $\pm$ 15.1 <sup>b</sup>
$CO_{2air}$ , $\mu mol \cdot mol^{-1}$	389.8 $\pm$ 0.7 <sup>a</sup>	391.2 $\pm$ 0.8 <sup>a</sup>
$T_{air}$ , °C	27.1 $\pm$ 0.2 <sup>a</sup>	22.4 $\pm$ 0.2 <sup>b</sup>
VPD, KPa	2.2 $\pm$ 0.04 <sup>a</sup>	1.3 $\pm$ 0.02 <sup>b</sup>
$T_{soil}$ , °C	15.8 $\pm$ 0.2 <sup>a</sup>	12.9 $\pm$ 0.2 <sup>b</sup>
VWC, % vol.	11.2 $\pm$ 0.1 <sup>a</sup>	15.8 $\pm$ 0.1 <sup>b</sup>
$C_{tot1}$ , %	24.1 $\pm$ 0.7 <sup>a</sup>	38.6 $\pm$ 0.2 <sup>b</sup>
$C_{tot2}$ , %	0.1 $\pm$ 0.0 <sup>a</sup>	0.3 $\pm$ 0.0 <sup>b</sup>
$N_{tot1}$ , %	0.4 $\pm$ 0.1 <sup>a</sup>	0.9 $\pm$ 0.1 <sup>b</sup>
$N_{tot2}$ , %	0.1 $\pm$ 0.0 <sup>a</sup>	0.1 $\pm$ 0.0 <sup>a</sup>
$pH_{KCl}$	4.7 $\pm$ 0.1 <sup>a</sup>	3.8 $\pm$ 0.1 <sup>b</sup>
Soil	Albic Podzol (Arenic) <sup>a</sup>	Albic Podzol (Arenic) <sup>a</sup>
Tree stand age, years	10 <sup>a</sup>	95 <sup>b</sup>

among plants of the herb-subshrub layer. The distance between rings was 2–3 m. Measurements of  $CO_2$  flux from soil surface in both SPs were taken during 90 seconds with 30 second intervals, according to the system's standard configuration, in three replications for each ring, every 10 days. Soil temperature and volumetric water content were measured in the 0–20 cm layer at each ring.

### Statistical analysis

The data were statistically processed with Statistica 13.3 (TIBCO Software Inc., USA). Differences were considered significant at  $p < 0.05$ . The survey year effect being insignificant ( $p > 0.05$ ), we pooled together the datasets on tree and soil characteristics over the 3 years of observations. The annual total numbers of measurements of leaf photosynthesis and dark respiration rates and  $CO_2$  flux from soil surface were 600, 600, and 144, respectively. The variability of a trait was quantified by the coefficient of variation (CV, %). Significant differences between means were estimated by the Tukey's test.

## Results

### $CO_2$ gas exchange in plants

The photosynthesis rates of the leaf and one-year-old needles in the advance regeneration of deciduous species and pine were the highest in the clear-cut site (Fig. 2). Their values under the forest canopy were significantly lower: by 36, 28, 27, and 25% for birch, alder, aspen, and pine, respectively. At the same time, the leaf dark respiration rate was highly stable in all the deciduous species, irrespective of the phytocoenotic environment. Dark respiration in pine, on the contrary, was 40% higher under the forest canopy versus the clear-cut site. Furthermore, pine compared to deciduous species had lower rates of both photosynthesis (2.3 times lower in both sample plots), and respiration – 1.7 and 1.2 times lower in the clear-cut site and in the pine stand, respectively.

Analysis of the data on the foliar uptake (photosynthesis) and emission of CO<sub>2</sub> (respiration) by young plants showed that leaves of birch, alder and aspen in the clear-cut site can fix 8–10 times more CO<sub>2</sub> than they release through dark respiration. Needles of pine trees in the clear-cut site metabolize assimilates less sparingly than deciduous species, assimilating only 6 times as much carbon dioxide as is released through respiration. This tendency for more economical photosynthesis in deciduous species compared to pine persists under the forest canopy (6:1 and 3:1, respectively).

Another noteworthy fact is that in the three years of observations, within-season variability (date-specific) of the investigated indices of CO<sub>2</sub> exchange in woody plants in the clear-cut site and under the bilberry pine forest canopy was high while variation among years was low ( $p > 0.05$ ). The variability (CV, %) of the photosynthesis rate in all tree species in the clear-cut site and under the forest canopy was 27–33 and 28–45%, respectively, and that of foliar dark respiration was 23–30% in both sample plots.

### **Soil respiration**

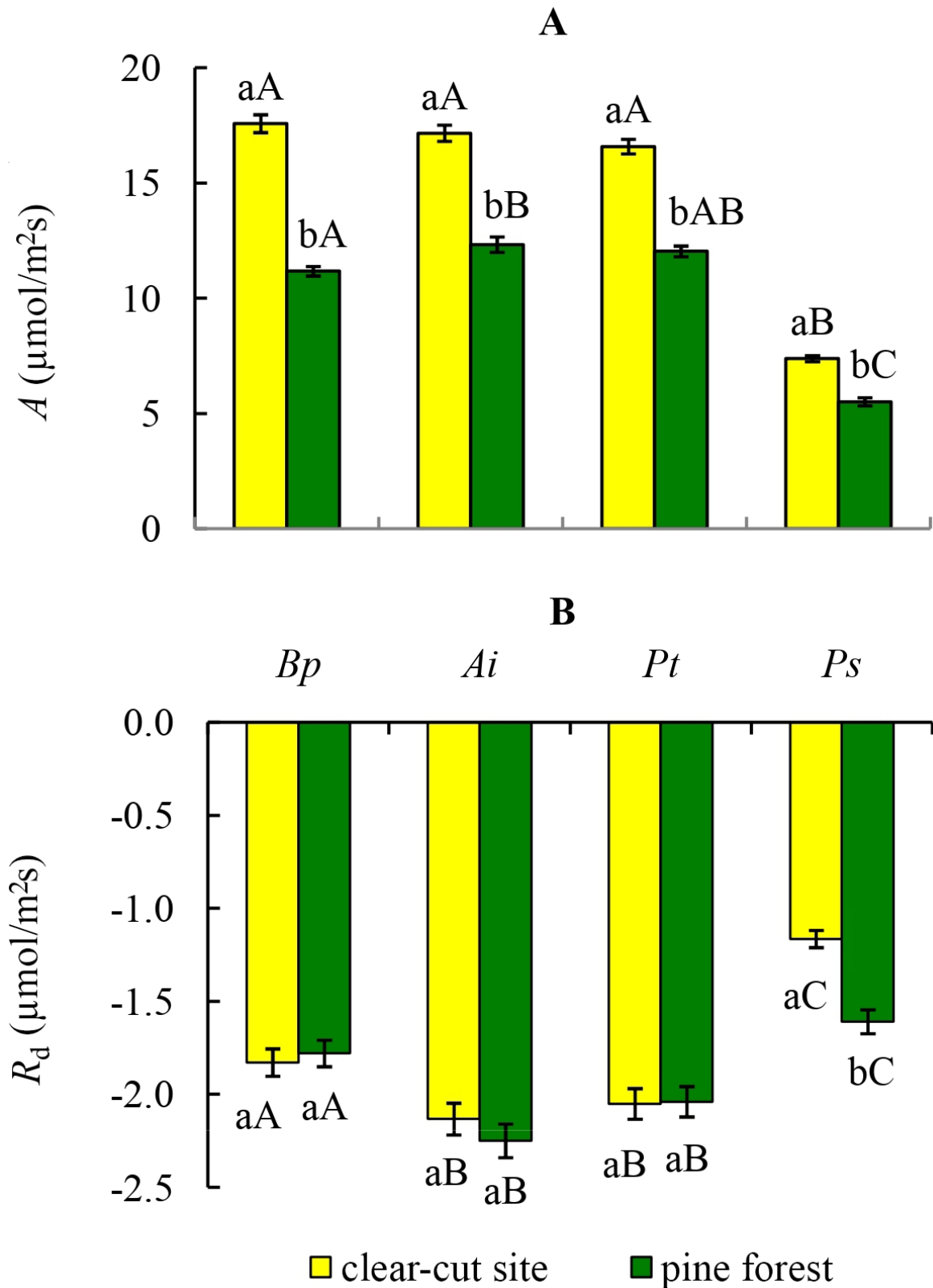
According to our data, the microgroup with fine woody debris SP 1<sub>3</sub> featured 6% higher soil temperatures than the other two microgroups in the clear-cut site (Fig. 3). Soil temperature in the bilberry pine stand SP 2 was 21% lower than in the clear-cut site because of lower mean daytime illumination and surface air temperature (Table 1). At the same time, SP 2 in the mature tree stand had a 58% higher soil water content compared to the clear-cutting's microgroups with true-moss-dominated ground vegetation SP 1<sub>2</sub> and with fine woody debris SP 1<sub>3</sub>. These features of the soil hydrothermal regime in the surveyed sites may be responsible for the 30% higher CO<sub>2</sub> flux from soil surface in the bilberry pine stand versus the clear-cut site. On the other hand, CO<sub>2</sub> flux from the soil surface in the undisturbed forest site was somewhat less variable over the 3-year study period (CV = 18%) compared to that in the clear-cut site (CV = 23%). Importantly, 10 years after clear-cutting, the different microgroups of ground vegetation (herbaceous SP 1<sub>1</sub> and true-moss-dominated SP 1<sub>2</sub>) or its absence (fine woody debris SP 1<sub>3</sub>) had no significant effect on the level of CO<sub>2</sub> emission from soil surface in the site.

### **Discussion**

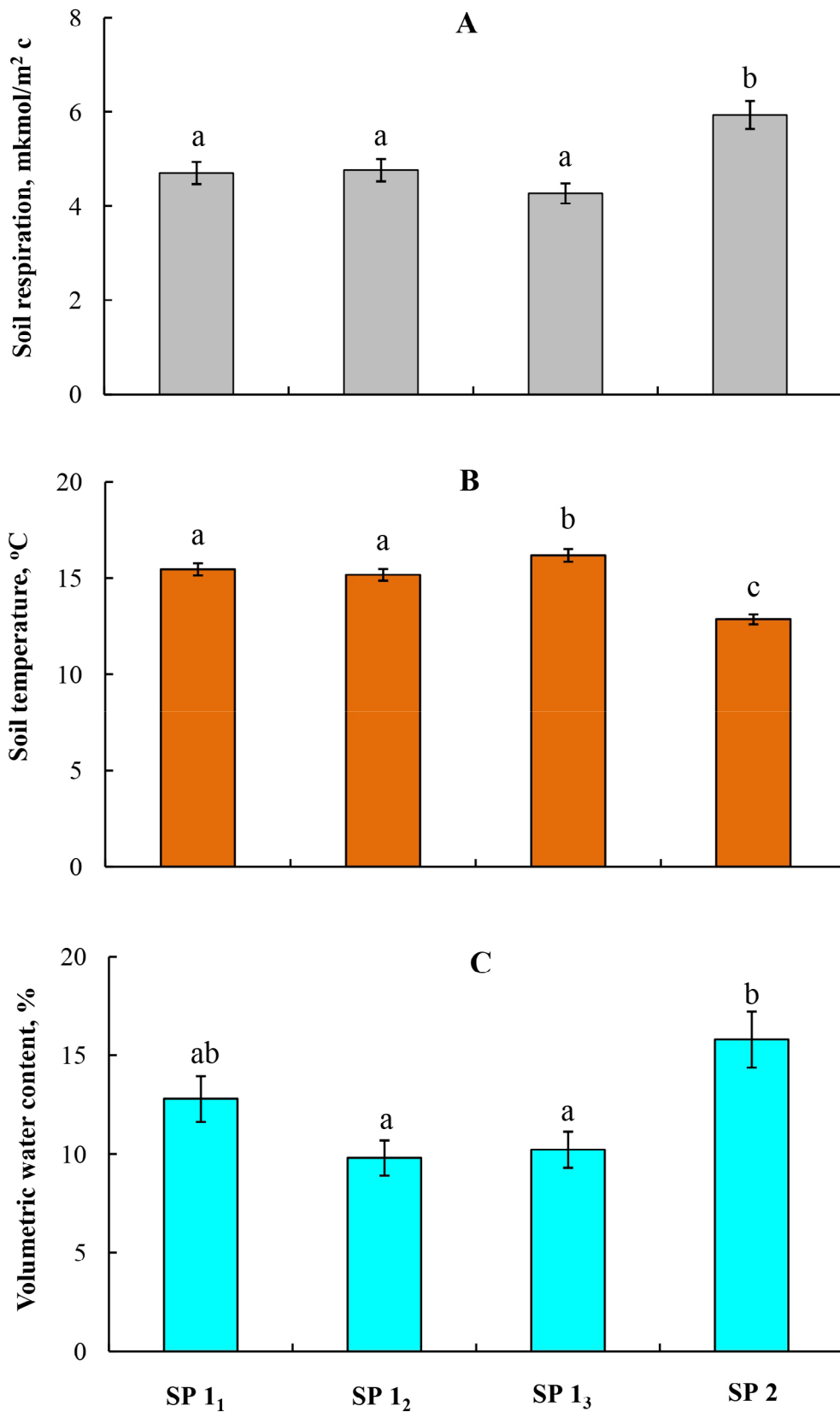
Plant photosynthesis and soil respiration largely govern the carbon balance of terrestrial ecosystems (Kudeyarov et al., 2007; Olchev et al., 2017). Major removal of photosynthesizing biomass from the forest ecosystem during clear-cutting has profound effects on the ecological, meteorological, and hydrological conditions in the ecosystem (Dymov, 2017; Keeman and Kimmins, 1993; Olchev et al., 2009). We demonstrated (Table 1) that during the survey period the microclimate of the clear-cut site featured higher mean daytime PAR (5-fold), vapor pressure deficit (1.7-fold), air and soil temperatures (1.2-fold) compared to the undisturbed pine forest site. Previously, we have also observed the change in the ecological conditions upon clear-cutting to entail a notable decline in the percentage cover of typical forest species in the herb-subshrub layer (*Convallaria majalis*, *Melampyrum pratense*, *Vaccinium myrtillus*) coupled with an obvious degradation of the moss-lichen layer and, on the contrary, a 10–20-fold increase in the abundance of species that are usually suppressed under forest canopy (*Calamagrostis arundinacea* and *Chamaenerion angustifolium*) (Pridacha et al., 2021).

### **CO<sub>2</sub> gas exchange in plants**

The light dependence of CO<sub>2</sub> gas exchange in plants is species-specific and variable at daily, seasonal, and annual scales (Lambers and Oliveira, 2019; Larcher, 2003; Sazonova et al., 2011; Suvorova, 2009; Tselniker et al., 1993), reflecting the high plasticity of this process in general. Inter-species differences in photosynthesis parameters are determined by the specific features of the leaf mesostructure and ontogeny in different species. The rise in the rate of photosynthesis observed in pine and deciduous trees (Fig. 2) growing in open clear-cut areas with sufficient light is possibly due to the formation of thicker leaves containing more nitrogen per unit leaf area (Poorter et al., 2019; Utkin et al., 2008). This assumption was corroborated by our previous findings that the specific content of nutrients in leaves was the highest and specific leaf area (SLA), on the contrary, was the lowest in all plant species in the clear-cut site versus closed-canopy forest site (Pridacha et al., 2021). Such structural and functional transformations in plants are adaptive in nature, since an increase in leaf area in response to poor illumination under forest canopy, vice versa, serves to stabilize biomass increment (Niinemets, 2010; Tselniker et al., 1993).



**Fig. 2.** Rates of photosynthesis (A) and dark respiration (B) of a leaf in *Betula pendula* (*Bp*), *Alnus incana* (*Ai*), *Populus tremula* (*Pt*) and one-year-old needles of *Pinus sylvestris* (*Ps*) in the clear-cut site and under forest canopy in July 2017–2019 (showing means and their standard errors). Different lowercase letters (a, b) indicate significant ( $p < 0.05$ ) within-species differences in the means between the two SPs, and different uppercase letters (A, B, C) indicate significant ( $p < 0.05$ ) inter-species differences in the means within each SP.



**Fig. 3.** Mean daytime values of CO<sub>2</sub> flux from soil surface (A), soil temperature (B), and volumetric water content in the 0–20 cm soil layer (C) in July and August 2017–2019 (showing means and their standard errors). SP 1<sub>1,2,3</sub> – a clear-cut site with account for ground vegetation microgroups (herbaceous, true-moss, fine woody debris, respectively), SP 2 – bilberry-type pine stand. Different lowercase letters (a, b) indicate significant differences between the means across microgroups in the sample plot ( $p < 0.05$ ).

The elevated level of dark respiration in pine under forest canopy compared to the clear-cut site, which is not found in deciduous species, can be explained by their different shade adaptation capacities (Sazonova et al., 2011; Suvorova, 2009; Tselniker et al., 1993), as well as by differences in the ontogenesis of gymnosperm needles and angiosperm leaves, in particular the different formation rates and duration (Kishchenko, 2000; Kishchenko and Vantenkova, 2013). On the other hand, the lower photosynthetic productivity of pine versus deciduous species is apparently associated with the functional characteristics of plants belonging to different phylogenetic groups, namely the leaf life span (Shiklomanov et al., 2020; Vasilov, 2015). As compared to deciduous trees, the prolonged duration of active photosynthesis in conifers slows down the rate at which the leaf photosynthetic potential is realized.

A likely explanation of the similarity of the multiannual means of CO<sub>2</sub> gas exchange indices between trees in the clear-cut site and under the bilberry pine forest canopy is the narrow range of variation of hydrothermal conditions in the 2017–2019 growing seasons and the absence in the study period of extreme weather events (heat, drought, flood, etc.), which could have significantly influenced the investigated parameters.

### **Soil respiration**

It is especially interesting to study the spatial heterogeneity of soil respiration and the factors behind it. We have previously noted the high acidity and the poor nutrient status of soils in both the clear-cut site and the undisturbed bilberry pine forest (Pridacha et al., 2021), which is in agreement with known data on the low fertility of forest soils in Karelia (Morozova and Fedorets, 1992). The relatively high C/N ratio in the top organic horizon of soils in the clear-cut site (65) and the pine stand (44) is also indicative of the tense nitrogen nutrition regime in both communities and the generally low rate of organic matter mineralization. Meanwhile, the higher rate of soil respiration in the natural stand in our study (Fig. 3) can apparently be attributed to the contribution of the forest floor (Chi et al., 2021; Morén and Lindroth, 2000) and higher contribution of autotrophic respiration due to greater root biomass in mature trees which is evenly distributed in mineral horizons (Pridacha et al., 2021), as well as to a higher soil water content compared to the clear-cut site (Pumpanen et al., 2008). It also appears probable that heterotrophic respiration contributes more to total CO<sub>2</sub> emission from the soil surface in the bilberry pine stand versus the clear-cut site due to higher rhizomicrobial respiration (Baldrian, 2017; Luo and Zhou, 2010).

The lower volumetric water content of soil in the clear-cut site is obviously associated with the higher mean diurnal illumination and vapor pressure deficit (Table 1), as well as the higher stomatal conductance and leaf transpiration rate in trees growing in the clear-cut site versus the undisturbed forest stand (Pridacha et al., 2021), as previously stated in (Olchev et al., 2009; Radler et al., 2010; Williams et al., 2014). The fact that soil temperatures were the highest in the microgroup with fine woody debris in the clear-cut site can be explained by the higher activity of the microbial community during the decomposition of plant residues (Baldrian, 2017; Luo and Zhou, 2010). At the same time, the lower variability of the CO<sub>2</sub> flux from soil surface in the bilberry pine stand versus the clear-cut site is in conformance with our data regarding more homogenous ground vegetation in the natural stand, which comprised 37 taxa of mosses, lichens, and vascular plants versus 56 taxa in the clear-cut site (Pridacha et al., 2021).

An important note is that in spite of the highly motley and mosaic soil cover and heterogeneous soil respiration (Kudeyarov et al., 2007; Luo and Zhou, 2010; Mukhortova et al., 2021), our own data on CO<sub>2</sub> emission from soil in the clear-cut site and the mature bilberry pine stand in southern Karelia are quite comparable to the soil respiration levels reported for middle-aged pine stands in Finland (Niinistö et al., 2011) and Middle Siberia (Makhnykina et al., 2020). Assessments of the seasonal patterns in CO<sub>2</sub> fluxes from the soil surface in boreal pine stands revealed soil emission to be the highest in the period from mid-July until late August (Makhnykina et al., 2020; ; Morén and Lindroth, 2000; Osipov, 2015; Yalynskaya, 1999), which is attributed to the effect of the seasonal dynamics of soil temperatures on the functional activity of autotrophic and heterotrophic organisms (Kurganova et al., 2020; Laganierie et al., 2012; Yuste et al., 2003). This fact provides the ground to regard the reported levels of CO<sub>2</sub> flux from the soil surface in the regenerating clear-cutting of a bilberry pine stand and in the undisturbed forest site as the reference levels for the warm period of the year in the given biogeocoenotic settings.

Thus, based on the analysis of 3-year averages for the components of the carbon exchange of woody plants and soils in a 10-year-old clear-cut site and under bilberry-type pine forest canopy in the warm time of the year in southern Karelia, we can infer that photosynthetic CO<sub>2</sub> uptake by trees prevails over its release through soil respiration in both sample plots. This appears to be an important result, considering the lack of common understanding regarding the temporal dimension of the clear-cutting

effect on the capacity of forest ecosystem to sequester or release CO<sub>2</sub> (Amiro et al., 2010; Mamkin et al., 2019; Vestin et al., 2020; Williams et al., 2014; Zha et al., 2009). The results of our previous field studies of the components of CO<sub>2</sub>/H<sub>2</sub>O exchange in coniferous and deciduous trees on automorphic sandy soils in southern Karelia (Pridacha et al., 2019) have been used for parametrization of the rates of photosynthesis, respiration, and stomatal conductance of pine and birch in the MixFor-SVAT model (Olchev et al., 2017) and to calculate possible changes in CO<sub>2</sub> and H<sub>2</sub>O fluxes in Karelian pine forest ecosystems under future climate change. Modeling suggests the integral CO<sub>2</sub> exchange and evapotranspiration of Karelian pine forests will tend to grow (by 39 and 5%, respectively) under the climate scenario (A1B) simulating a moderate rise in mean annual air temperature (by 3.4 °C) in the region by the end of the 21<sup>st</sup> century (Pridacha et al., 2019).

## Conclusions

The reported study demonstrated a significant effect of clear-cutting on components of the carbon balance in the boreal forest ecosystem. We determined the specific values of CO<sub>2</sub> photosynthetic fixation and its release through dark respiration in the main forest tree species of North European Russia, as well as of CO<sub>2</sub> emission from the soil surface in a clear-cut site and under the canopy of a bilberry-type pine stand during the warm time of the year. The dominance of CO<sub>2</sub> fixation through photosynthesis over its release through dark respiration (6–10-fold) was greater in pine and deciduous species in the clear-cut site than under forest canopy (3–6-fold). Soil emission in the 10-year-old clear-cut site was shown to contribute less (1.3-fold) to the atmospheric CO<sub>2</sub> flux than it does in the mature bilberry pine forest site. We revealed the patterns to be applied to local phytocoenotic and climatic conditions. These results can serve as the basis for predictive assessments of human impact on the carbon exchange of vegetation and soils in forest ecosystems at different spatial and temporal scales.

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