Carbon and Oxygen Gas Exchange in Woody Debris: The Process and Climate-Related Drivers

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Abstract: The carbon-to-oxygen relationship and gas exchange balance, organic carbon to CO 2 conversion intensity and efficiency, and their relevance to climate parameters and wood decay fungi were investigated for birch woody debris (WD) in the Mid-Urals mixed pine and birch forests. It was shown that, within the range of temperatures from 10 to 40 °C and relative moisture (RM) of wood of 40% and 70%, aerobic gas exchange was observed in the WD, encompassing the physiologically entwined processes of CO 2 emission and O 2 uptake. Their volumetric ratio (0.9) confirmed that (1) the WD represents a globally significant CO 2 source and appropriate O 2 consumer and (2) the oxidative conversion of organic carbon is highly efficient in the WD, with an average ratio of CO 2 released to O 2 consumed equal to 90%. The balance of carbon-to-oxygen gas exchange and oxidizing conversion efficiency in the WD were not affected by either fungal species tested or by moisture or temperature. However, the intensity of gas exchange was unique for each wood decay fungi, and it could be treated as a climate-reliant parameter driven by temperature (Q 10 = 2.0–2.1) and moisture (the latter induced a corresponding trend and value changes in CO 2 emission and O 2 uptake). Depending on the direction and degree of the change in temperature and moisture, their combined effect on the intensity of gas exchange led to its strengthening or weakening; otherwise, it was stabilized. Aerobic respiration of wood decay Basidiomycetes is an essential prerequisite and the major biotic factor in the WD gas exchange, while moisture and temperature are its climatic controllers only.

Keywords: boreal forest; woody debris; CO 2 ; O 2 ; gas exchange; temperature; moisture; wood decay Basidiomycetes

1. Introduction

Forests are the largest terrestrial carbon sinks and reservoirs, playing an important role in CO 2 regulation in the atmosphere. Their carbon cycle is specified by a large-scale and long-lasting (from dozens to hundreds of years) woody pool. It is estimated at 30 Gt C for the forests of Russia, and 240 Mt are annually added to it. Mobilization of woody pool carbon, shown by biological decomposition of woody debris (WD), is the main process of the forest ecosystem carbon cycle. The WD reservoir is almost 5 Gt of carbon equivalent in Russia, second to soil with 214 Mt C-CO 2 annual releases to the atmosphere [1]. Therefore, forest ecosystems are not only C-CO 2 removers, but they also are among the largest natural sources of this greenhouse gas, whose accumulation in the atmosphere is attributed to the modern climate change [2]. That is the rationale for intensive studies of WD decomposition and gas exchange.
Although performed in numerous areas, previous research mainly focused on CO$_2$-emission activity of WD and its relevance to climate [3–18]. The results of these studies clearly confirm that humidity and temperature are the most important climatic drivers of CO$_2$ gas exchange in WD and climate change that are projected to increase precipitation and temperature [19], which should significantly affect WD carbon respiration. Alongside the variety of research examining WD respiration, the vast majority is lacking assessment of connectivity with (1) oxygen gas exchange and (2) the activity of certain species and groups of organisms that decompose wood. In particular, only a few works available consider the relationship between communities of wood decay fungi and CO$_2$ emission intensity of WD [20–24]. The relationship and balance of carbon-oxygen gas exchange in WD under its decomposition by xylotrophic Basidiomycetes are considered only in Solovyov’s monograph [25].

WD is a biologically inactive dead mass, and its gas exchange is a consequence of the myco-bacterial community populating it. Xylotrophic Basidiomycetes (Basidiomycota, Agaricomycetes) dominate this community, being the only organisms in the modern biosphere capable of biochemical conversion of lignocellulose. Their activity provides a major contribution to gas exchange and decomposition of WDs [1,26–32]. Xylotrophic Basidiomycetes are accompanied by mycophilous fungi and bacteria that are capable of developing in this specific environment formed by xylotrophic fungi [1,33,34]. They include not only aerobic but also anaerobic microorganisms, so far as anaerobic conditions could locally form in timber owing to high moisture and O$_2$ uptake by fungi uncompensated by diffusion. Such conditions promote the formation of anaerobic bacteria and archaea, as well as the anaerobic production of CO$_2$ and CH$_4$ as gas exchange [1,4,18,20,35]. There is evidence that methane may also be produced by xylotrophic Basidiomycetes [36,37], many of which can exist in oxygen-free environments [25,38], being de facto electively anaerobic organisms. The latter results in a complex and diverse nature of gas exchange in WD, where qualitative and quantitative features are regulated by appropriate features of xylotrophic myco-bacterial communities and the environment parameters such as temperature and humidity. In view of the recent challenge of climate change, it is evident that the investigation of gas exchange in WD as a multicomponent process and its intensity and relevance to composition of wood decay agents and climate has become highly urgent.

With this, the objectives of our work comprised the investigation of (1) contingency and balance of carbon to oxygen gas exchange in the WD; (2) intensity and efficiency of organic carbon conversion into CO$_2$; and (3) the relation of CO$_2$ and O$_2$ gas exchange with climate parameters and wood decay fungi.

2. Materials and Methods

The studies were carried out in pre-forest and steppe mixed pine and birch forests with _Pinus sylvestris_ L. and _Betula pendula_ Roth in the Sysert district of the Sverdlovsk region, 56°36′5″ N and 61°3′24″ E. The local climate is temperate continental with annual mean temperature range of +1.5 to +0.1 °C. The warmest month is July (+17 °C) and the coldest is January (−16 °C). The permanent snow cover lasts from November to April, while the growth season is from May to September. The annual precipitation is 350–400 mm, with most of it during summer and fall.

**Experimental Design**

The carbon and oxygen gas exchange was assessed for birch WD (_B. pendula_), with wood decay fungi basidiocarps of the following eight species: _Daedaleopsis tricolor_ (Bull.) Bondartsev and Singer; _Fomes fomentarius_ (L.) Fr.; _Fomitopsis betulina_ (Bull.) B.K. Cui, M.L. Han and Y.C. Dai; _Hapalopilus rutilans_ (Pers.) Murrill; _Stereum hirsutum_ (Willd.) Pers.; _Steccherinum ochraceum_ (Pers. ex J.F. Gmel.) Gray; _Trametes pubescens_ (Schumach.) Pilát; and _T. versicolor_ (L.) Lloyd. They form a wood-decay fungi complex common to _Betula_ WD of mixed birch and pine forests of the pre-forest–steppe zone. The identification of the
fungi species was carried out with the use of regular mycological methods [39,40], and the terminology is provided in accordance with MycoBank Database [41].

Gas analysis was carried out for the samples of wood (4 cm in diameter and 3 cm in length, average size; and mean volume 0.03 L) that are defined as fine, woody debris in, accordance with Enrong et al. [42]. The samples were cut with the use of a tree chain saw from sites of birch twigs and stems, close to the basidiocarps of the fungi species referred to above. Then, the samples were cleaned from remnants of leaves, needles, herbaceous plants, and fungi basidiocarps and weighed with Kern 440-45N weight (Kern & Sohn GmbH, Germany, 0.1-g precision) to determine the initial wet mass. To calculate the cubic content, the diameters and length of each sample were measured.

The thermal relationship of carbon-to-oxygen gas exchange was analyzed at 10, 20, 30, and 40 °C ± 1 °C and two wood relative moisture (RM) levels of 37–41% (average 40%), which correspond to the initial natural wood moisture, and 61–77% (average 70%) when the samples were wetted with distilled water to simulate increased humidity conditions. The wood absolute moisture (AM) for the first case was 65%, and it was 245% for the second case, accordingly. The sample moistures were controlled throughout the entire gas analysis by their wet mass. Upon completion of the experimental measurement cycles, the samples were oven dried at +105 °C for 72 h to determine their absolute dry mass and moisture. The RM and AM were correspondingly calculated with the use of Equations (1) and (2):

\[
RM = \frac{(M_{W} - M_{d})}{M_{W}} \times 100\%,
\]

where \( RM \) is the relative moisture, in percent; \( M_{W} \) is the mass of wet sample, in g; and \( M_{d} \) is the absolute dry weight of the sample, in g.

\[
AM = \frac{(M_{W} - M_{d})}{M_{d}} \times 100\%,
\]

where \( AM \) is the absolute moisture, in percent; \( M_{W} \) is the mass of wet sample, in g; and \( M_{d} \) is the absolute dry weight of the sample, in g.

The design of the gas analysis was as follows. The open-exposure chambers with prepared samples of wood (three chambers with the same fungi species, one sample per chamber) with an average RM/AM equal to 40/65% were initially put in a thermostat for 2 h to reach the required temperature (+10 °C at the first stage). Then, the chambers were sealed and the initial CO₂ and O₂ concentrations were measured inside the chambers. The chambers were consequently exposed in the thermostat under the same temperature (+10 °C) for about 3 h. In due time of the exposition, the concentration of gases in the chambers decreased (O₂); otherwise, it increased (CO₂) by 1 to 2 volumetric percent, which enabled it to avoid the negative effects of hypoxia and hypercapnia within the gas exchange. At the end of the exposition period, the concentrations of CO₂ and O₂ in the chambers were measured again. After that, the chambers were opened, and the samples were removed, weighed, and, if necessary, moistened with distilled water to the initial weight, placed in the same chambers, and the above-described cycle was consequently repeated at 20, 30, and 40 °C. Similar exposure cycles and measurement procedures were performed for the same wood samples under RM/AM equal to 70/245%, as appropriate. The first moisture level corresponded to an average (42%) and the second level corresponded to the highest (68%) RM of WD of in the pre-forest and steppe mixed pine and birch forests [15].

The concentrations of O₂ and CO₂ were measured in volumetric percent (ϕ) with the use of CO₂/O₂ infrared electrochemical gas analyzer with built-in automated flow-type sampling controller and data processor (Micro-sensor Technique Ltd., Russian Federation, precision ± 0.2%). Carbon-to-oxygen gas exchange was estimated based on O₂ and CO₂ concentration differences in the chambers at the beginning and the end of the exposition period, with an account of the sample volumes (Equation (3)) and the duration of the exposition (Equation (4)):

\[
\varphi_{v} = \frac{(V_{1} - V_{2})}{V_{1} \times \varphi_{reg}},
\]
where $\varphi$—$\text{CO}_2/O_2$ volumetric percent is calculated with a count of the sample volume; $V_1$ is the volume of the exposure chamber (0.3 l); $V_2$ is the sample volume, in L; and $\varphi_{reg}$ is experimental chamber measurements of volumetric percent of CO$_2$ emitted / O$_2$ consumed.

$$\varphi_{ct} = \varphi_{v}/T_{exp} \times 60 \text{ min}, \tag{4}$$

where $\varphi_{ct}$—$\text{CO}_2/O_2$ is the volumetric percent calculated with a count of the sample volume and exposition period; $\varphi_{v}$ (see Equation (3)); and $T_{exp}$ is the time of exposure, in min.

The estimates of gas exchange for WD are presented in Table A1. They were used for the analysis of the correlation between CO$_2$ emission and O$_2$ uptake, and the ratio of volumes of CO$_2$ emitted and O$_2$ consumed (CO$_2$ to O$_2$ ratio). The CO$_2$ emission activity for woody debris was calculated with the use of Equation (5):

$$\text{ECO}_2 = \Delta \text{CO}_2 \times (V_1 - V_2)/V_m \times M_1/M_2 \times 0.27 \times 273/T, \tag{5}$$

where ECO$_2$ is emission activity, $\mu$g C-CO$_2$ g dry wood mass$^{-1}$ per hour ($\mu$g C-CO$_2$ g$^{-1}$ h$^{-1}$); $\Delta \text{CO}_2$ is the CO$_2$-specific emission from the sample within the exposition period, in ppm/h; $V_1$ is the volume of the exposure chamber (0.3 l); $V_2$ is the sample volume, in L; $V_m$ is the molar volume (22.4 L/mol); $M_1$ is the molar mass of CO$_2$ (44 g / mol); $M_2$ is the dry mass of the wood sample, in g; and $T$ is the air temperature (K).

Similarly, the intensity of oxygen uptake was calculated by Equation (6):

$$\text{EO}_2 = \Delta \text{O}_2 \times (V_1 - V_2)/V_m \times M_1/M_2 \times 273/T, \tag{6}$$

where EO$_2$ is the intensity of oxygen uptake, $\mu$g O$_2$ g dry mass$^{-1}$ of wood per hour ($\mu$g O$_2$ g$^{-1}$ h$^{-1}$); $\Delta \text{O}_2$ is the O$_2$-specific uptake by the sample within the exposition period, in ppm/h; $V_1$ is the volume of the exposure chamber (0.3 l); $V_2$ is the sample volume, in L; $V_m$ is the molar volume (22.4 L/mol); $M_1$ is the molar mass of O$_2$ (32 g/mol); $M_2$ is the dry mass of the wood sample, in g; and $T$ is the air temperature (K).

Statistical treatment of the results was performed with the use of Statistica 8.0 software (Stat Soft Inc., Tulsa, OK, USA). Arithmetic means (m) are provided with standard error (SE). The comparison of average values and assessment of significance of environmental factors was performed with the use of the one-way ANOVA test. The significance of the relationship between the variables was estimated with the Pearson correlation factor ($r$) at the confidence level of ($p$) < 0.05.

3. Results

3.1. Relationship between the CO$_2$ Emission and O$_2$ Uptake in Gas Exchange of WD

In gas exchange of WD, O$_2$ and CO$_2$ fluxes were positively correlated ($r =$ 0.83–0.97) and not temperature dependent. Thus, the correlation between O$_2$ consumed and CO$_2$ released was 0.88 for wood RM 40% and temperature +10 °C; it was 0.93 for the temperature of 20 °C, 0.91 for 30 °C, and 0.96 for 40 °C. For wood RM 70%, the same pattern was observed: The correlation was 0.96 for the temperature +10 °C and it was 0.97 for +20 °C, 0.84 for +30 °C, and 0.93 for +40 °C (Figure 1).

The degree of contingency between the volume of O$_2$ consumed and CO$_2$ emitted did not depend on wood moisture. This was confirmed by the close correlation factors derived for O$_2$ and CO$_2$ fluxes under similar temperatures but different RMs (40% and 70%): They were 0.88 and 0.96 for +10 °C, 0.93 and 0.97 for +20 °C, 0.91 and 0.84 for +30 °C, and 0.96 and 0.93 for +40 °C, correspondingly (Figure 1). A similar positive correlation was found for CO$_2$ and O$_2$ fluxes and gas exchange in wood affected by white (Fomes fomentarius) and brown (Fomitopsis betulina) rot: The values of the factors were 0.79–0.85 and 0.84–0.82 for wood with RM 40% and 70%, correspondingly (Figure A1).
The CO2-to-O2 ratio (CO2:O2) for gas exchange of WD decomposed by wood decay fungi varied from 0.4 to 2.1, but in the majority of cases (80%) it did not exceed 1.0. The highest values (1.4–2.1) were sporadically observed under the RM of 70% and the temperature +20 °C (Figure 1). The factor analysis showed no significant relationship between the CO2-to-O2 ratio and the WD rot type. Indeed, the CO2-to-O2 ratio was significantly higher for wood with RM 40%: $F(1,4) = 8.1574, p = 0.04$, and it was higher than for the RM of 40%. Significant differences were noted for a sole case of temperature equal to +20 °C and 40% RM of wood.

In some cases, the relationship between the CO2-to-O2 ratio and the moisture of woody debris was identified. For instance, the CO2-to-O2 ratio was significant for gas exchange in wood decomposed by *F. fomentarius* under the temperature of +20 °C and wood RM of 70%: $F(1,4) = 9.8968, p = 0.03$ (Table 1). However, in general, the ratio did not demonstrate any

**Figure 1.** The contingency of O2 and CO2 fluxes in gas exchange for *Betula* WD affected by xylotrophic Basidiomycetes under the RM levels of 40% (I) and 70% (II), the temperature +10 °C (a), +20 °C (b), +30 °C (c), and +40 °C (d); $R^2$ is the coefficient of determination.

### 3.2. Carbon-to-Oxygen Balance in WD Gas Exchange

The CO2-to-O2 ratio (CO2:O2) for gas exchange of WD decomposed by wood decay fungi varied from 0.4 to 2.1, but in the majority of cases (80%) it did not exceed 1.0. The highest values (1.4–2.1) were sporadically observed under the RM of 70% and the temperature of 20–40 °C (Table 1). The factor analysis showed no significant relationship between the CO2-to-O2 ratio and the wood decay fungi species. Significant differences were noted for a sole case of temperature equal to +20 °C and 40% RM of wood: $F(1,4) = 9.8968, p = 0.03$ (Table 1).

In some cases, the relationship between the CO2-to-O2 ratio and the moisture of woody debris was identified. For instance, the CO2-to-O2 ratio was significant for gas exchange in wood decomposed by *F. fomentarius* under the temperature of +20 °C and wood RM of 70%: $F(1,4) = 8.1574, p = 0.04$, and it was higher than for the RM of 40%. The opposite relationship was found for wood decomposed by *T. versicolor*. Under the temperature of +10 °C, the CO2-to-O2 ratio was significantly higher for wood with RM 40%: $F(1,4) = 12.880, p = 0.02$ (Table 1). However, in general, the ratio did not demonstrate any
significant relationship either with moisture or with temperature for the four temperature levels (Table 2).

Table 1. The carbon-to-oxygen balance (CO$_2$ to O$_2$ ratio) in gas exchange for Betula WD decomposed by xylotrophic Basidiomycetes.

| Species          | Moisture 40/65 per Cent | Moisture 70/245 per Cent |
|------------------|-------------------------|--------------------------|
|                  | Temperature, °C         | Temperature, °C          |
|                  | 10 20 30 40            | 20 30 40                 |
| 1                | 0.6 (0.12) 1.0 (0.14)   | 0.8 (0.04) 0.6 (0.01)    |
| 2                | 0.6 (0.10) 0.5 (0.08)   | 1.1 (0.31) 0.7 (0.12)    |
| 3                | 0.5 (0.05) 0.8 (0.03)   | 0.7 (0.03) 0.7 (0.21)    |
| 4                | 0.9 (0.36) 0.8 (0.09)   | 0.9 (0.12) 0.4 (0.06)    |
| 5                | 0.9 (0.11) 0.5 (0.03)   | 0.9 (0.07) 0.6 (0.09)    |
| 6                | 0.8 (0.01) 0.9 (0.06)   | 0.9 (0.14) 1.0 (0.40)    |
| 7                | 0.8 (0.25) 0.8 (0.13)   | 0.6 (0.19) 1.1 (0.26)    |
| 8                | 0.9 (0.04) 0.9 (0.08)   | 0.9 (0.06) 0.7 (0.05)    |

Values are the average from three replicates (±SE). Species: 1, Daedaleopsis tricolor; 2, Fomes fomentarius; 3, Fomitopsis betulina; 4, Hapalopilus rutilans; 5, Steccherinum ochraceum; 6, Stereum hirsutum; 7, Trametes pubescens; 8, T. versicolor.

Table 2. The carbon-to-oxygen balance (CO$_2$ to O$_2$-ratio) in gas exchange for Betula WD decomposed by xylotrophic Basidiomycetes and relevance to temperature and moisture the ANOVA test.

| Moisture, % | Temperature, °C | Relevance to Temperature |
|------------|-----------------|--------------------------|
|            | 10 20 30 40     |                          |
| 40/65      | 0.8 (0.06)      | 0.8 (0.04)               |
|            | 0.9 (0.07)      | 0.9 (0.07)               |
| 70/245     | 0.7 (0.07)      | 1.0 (0.14)               |
|            | 1.0 (0.10)      | 1.0 (0.11)               |
| Relevance to moisture | $F(1,46) = 0.93269$, $p = 0.33$ | $F(1,46) = 3.5991$, $p = 0.06$ | $F(1,46) = 0.66490$, $p = 0.42$ | $F(1,46) = 0.99514$, $p = 0.32$ |

Values are the average from 24 replicates (±SE).

3.3. Gas Exchange Intensity of WD

The CO$_2$-emission intensity of WD varied in a wide range, from 4.1 to 188 C-CO$_2$ µg g$^{-1}$ h$^{-1}$, and it was found to be relevant to three driving factors (Table 3). The first driving factor comprised the wood decay fungi species, whose activity resulted in different emission intensity from birch wood under the similar temperature and moisture levels. Thus, under the temperature +20 °C and RM of 40%, the intensity varied from 12.6 to 53 C-CO$_2$ µg g$^{-1}$ h$^{-1}$, with regard to a particular fungi species. However, it increased to 17.8 to 111.4 C-CO$_2$ µg g$^{-1}$ h$^{-1}$ with the rise of RM to 70%. The differences in emission intensity were quite stable for a particular fungi species. Based on exchange intensity under the temperature +20 °C and the RM of 40%, the woody samples could be subdivided into two groups. The first group included the samples of wood decomposed by D. tricolor, F. betulina, F. fomentarius, and T. pubescens, whose wood decay activity resulted in emission intensity up to 20 C-CO$_2$ µg g$^{-1}$ h$^{-1}$. The second group included H. rutilans, S. ochraceum, S. hirsutum, and T. versicolor, which caused the intensity above 20 C-CO$_2$ µg g$^{-1}$ h$^{-1}$. The same two groups were distinguished at the temperatures +10 °C and +30 °C, with small differences (Table 3). The ANOVA analysis confirmed a significant relationship between fungi species and emission intensity in WD both for 40% and 70% of wood RM: $F(7,88) = 6.8706$, $p = 0.001$ and $F(7,88) = 5.0721$, $p = 0.001$, correspondingly.
Table 3. The CO\textsubscript{2}-emission intensity of Betula WD decomposed by xylotrophic Basidiomycetes, C-CO\textsubscript{2} µg g\textsuperscript{−1} h\textsuperscript{−1}.

| Species | Moisture 40/65 per Cent | Moisture 70/245 per Cent |
|---------|-------------------------|--------------------------|
|         | Temperature, °C | Temperature, °C |         | Temperature, °C | Temperature, °C |
| 10 | 20 | 30 | 40 | 10 | 20 | 30 | 40 | 10 | 20 | 30 | 40 |
| 1 | 11.1 (1.03) | 18.8 (1.67) | 57.8 (1.99) | 67.6 (3.83) | 25.7 (3.26) | 52.7 (7.14) | 116.7 (11.10) | 118.6 (15.02) |
| 2 | 9.6 (0.94) | 12.6 (1.41) | 45.2 (5.62) | 42.5 (2.54) | 15.0 (1.19) | 43.1 (4.68) | 80.5 (11.62) | 132.7 (8.03) |
| 3 | 8.4 (0.41) | 13.7 (1.43) | 42.1 (3.69) | 47.4 (0.91) | 21.3 (0.41) | 40.5 (0.32) | 52.7 (7.14) | 52.7 (7.14) |
| 4 | 16.3 (6.16) | 37.1 (1.07) | 59.1 (10.27) | 73.6 (9.76) | 13.4 (1.16) | 44.1 (2.34) | 102.4 (46.35) | 109.5 (49.37) |
| 5 | 15.9 (0.26) | 29.7 (4.80) | 72.5 (1.21) | 82.7 (2.10) | 15.0 (1.19) | 43.1 (4.68) | 80.5 (11.62) | 132.7 (8.03) |
| 6 | 11.8 (0.43) | 29.4 (1.71) | 50.3 (2.56) | 41.9 (2.30) | 22.7 (5.71) | 17.8 (5.67) | 62.6 (3.26) | 56.3 (7.35) |
| 7 | 4.2 (1.03) | 17.1 (1.78) | 15.4 (1.60) | 22.7 (4.97) | 4.1 (0.68) | 18.3 (0.88) | 55.7 (0.75) | 87.6 (1.06) |
| 8 | 30.2 (0.31) | 53.0 (1.80) | 92.1 (15.85) | 131.3 (8.59) | 68.0 (26.95) | 111.4 (10.10) | 180.2 (7.88) | 188.0 (33.36) |

Values are the average from three replicates (±SE). Species: see Table 1.

Temperature is the second driver that showed a high and positive correlation with the gas exchange rate WD (Table A2). The reaction to change in temperature depended on the species of fungi. For example, with an increase from +10 to +20 °C, depending on the species, the intensity emission of CO\textsubscript{2} increased by 1.3–4.0 times for 40% RM and by 1.6–4.5 times for 70% RM (Table 3). On average, for all eight species of fungi, an increase in temperature from +10 to +20 °C caused an increase in WD gas exchange by 2.0 times, and from +20 to +30 °C by 2.1 times at 40% and 70% RM. However, the shift from +30 to +40 °C did not cause the significant enhancement of emission CO\textsubscript{2} (Table 4).

Table 4. The intensity of CO\textsubscript{2} emission by Betula WD decomposed by xylotrophic Basidiomycetes (O\textsubscript{2} µg g\textsuperscript{−1} h\textsuperscript{−1}) and its relevance to temperature and moisture, one-way ANOVA test.

| Moisture, Per Cent | Temperature, °C | Relevance to Temperature |
|--------------------|-----------------|--------------------------|
| 10 | 20 | 30 | 40 | 10 | 20 | 30 | 40 | 10 | 20 | 30 | 40 | F(3,92) = 27.704, p = 0.001 | F(3,92) = 27.992, p = 0.001 |
| 40/65 | 13.5 (1.66) | 26.4 (2.77) | 54.3 (4.88) | 63.7 (6.72) | F(1,46) = 3.8317, p = 0.05 | F(1,46) = 7.1444, p = 0.007 | F(1,46) = 17.124, p = 0.0001 | F(1,46) = 15.612, p = 0.0002 |
| 70/245 | 23.3 (4.76) | 45.5 (6.29) | 97.5 (9.24) | 112.1 (10.26) | F(1,46) = 3.8317, p = 0.05 | F(1,46) = 7.1444, p = 0.007 | F(1,46) = 17.124, p = 0.0001 | F(1,46) = 15.612, p = 0.0002 |

Values are the average from 24 replicates (±SE).

Wood moisture is the third factor that had a strong and positive effect on the CO\textsubscript{2} emission activity (Table 3), but it depended on the species of fungi, as in the case of temperature. The increase in RM from 40% to 70% resulted in a 2.2-times increase of gas exchange for WD affected by D. tricolor, F. fomentarius, F. betulina, T. pubescens, and T. versicolor. Meanwhile, for the other wood decay fungi (H. rutilus, S. hirsutum, S. ochraceum), no changes in emission intensity were observed (Table A3). Nevertheless, as follows from Table 4, the increase in RM of wood from 40% to 70% (1.8-fold) was followed by appropriate enhancement of CO\textsubscript{2} emission intensity (ca. 1.8-fold) for all four temperatures. The one-way ANOVA test confirmed a significant relationship between gas exchange and moisture of WD.

In the case of a unidirectional change in temperature and humidity, their joint effect on WD gas exchange was equal to the sum of the effects of each separately. Thus, an increase in the temperature from +10 to +20 °C and in the RM of wood from 40% to 70% provided for a 3.4-times enhancement of CO\textsubscript{2} emission: from 13.5 to 45.5 C-CO\textsubscript{2} µg g\textsuperscript{−1} h\textsuperscript{−1}. This corresponded to the sum of temperature and moisture effects that strengthened the average gas exchange intensity, compared to 1.7- and 2.0-fold enforcements provided by each driver separately (Table 4). For multidirectional and quantitatively different changes in moisture and temperature, their combined effect will be the difference between the effects of each
particular driver. Thus, when the temperature dropped from +30 to +10 °C, the emission became 4.1 times lower, but the decrease was partially offset by a 1.7-fold increase in RM from 40% to 70%. With this, the resulting decrease was 2.3 times only: from 54.3 to 23.3 C-CO$_2$ µg g$^{-1}$ h$^{-1}$ (Table 4). Due to different directions, the changes in moisture and temperature could compensate each other’s effects on gas exchange of WD. For instance, emission intensity dropped from 26.4 to 13.5 C-CO$_2$ µg g$^{-1}$ h$^{-1}$ with the decrease in temperature from +20 to +10 °C, but it increased from 13.5 to 23.3 C-CO$_2$ µg g$^{-1}$ h$^{-1}$ with RM rising from 40% to 70%. As a result, the final gas exchange remained at the same level (Table 4).

3.4. Oxygen Gas Exchange Activity of WD

The oxygen gas exchange of woody debris is also closely related to temperature and moisture. Within the range of +10 to +30 °C, an increase in temperature by 10 °C provided for a 1.9-fold enhancement in oxygen uptake under the RM of 40%, and for 1.5–1.9 times under the RM of 70%. The highest oxygen uptake was observed for the temperatures of 30–40 °C, the same as for the highest CO$_2$ emission. The increase in RM of wood from 40% to 70% (1.8 times) provided for an appropriate 1.8-fold increase in oxygen uptake for all four temperature levels. The cumulative effect of temperature and moisture was also clearly displayed, and it resulted in enhancement or weakening of oxygen gas exchange, with regard to direction of temperature and moisture trends (Table 5).

| Moisture, Per Cent | Temperature, °C | Relevance to Temperature |
|--------------------|-----------------|--------------------------|
|                    | 10              | 20                       | 30          | 40          |
| 40/65              | 48.9 (4.82)     | 94.2 (9.43)              | 181.7 (22.74)| 204.8 (21.14)| $F(3,92) = 19.932, p = 0.001$ |
| 70/245             | 102.9 (22.52)   | 154.8 (21.68)            | 297.2 (39.49)| 349.2 (44.46)| $F(3,92) = 11.906, p = 0.001$ |
| Relevance to moisture | $F(1,46) = 5.4869, p = 0.02$ | $F(1,46) = 6.5547, p = 0.01$ | $F(1,46) = 4.4203, p = 0.01$ | $F(1,46) = 8.6103, p = 0.005$ |

Values are the average from 24 replicates (±SE).

3.5. Gas Exchange of Basidiocarps of Wood Decay Fungi

The fluxes of O$_2$ consumed and CO$_2$ released were closely and positively mutually related in the respiratory gas exchange of basidiocarps of brown (F. betulina) and white (D. tricolor) rot fungi ($r = 0.98$ and 0.99, correspondingly). They showed similar regularities in terms of CO$_2$ and O$_2$ volumetric ratio that was independent from temperature, being 0.8–0.9 under the range +10 to +40 °C, the same as for gas exchange of WD (Table 6). The CO$_2$ emission intensity of D. tricolor basidiocarps, on average, was lower (451.8 ± 51.5 µg g$^{-1}$ h$^{-1}$) than for F. betulina (991.6 ± 114.5 µg g$^{-1}$ h$^{-1}$), $F(1,22) = 18,466, p = 0.0003$. However, in both cases it was manifold higher than for WD that they decomposed (Table 3). The same as for wood. Emission intensity of basidiocarps was closely and positively related to temperature ($r = 0.66–0.77$): The rise of temperature by 10 °C, in the range +10 to +30 °C, increased their emission intensity by 1.5–2.3 times. The highest respiration activity of basidiocarps occurred the same as for WD temperature +30 °C, while at +40 °C, the gas exchange dropped by 25%–30% (Table 6), which was different from the exchange of WD that had the highest activity under 30–40 °C (see Table 4).
Table 6. The carbon-to-oxygen balance (CO\textsubscript{2} to O\textsubscript{2} ratio) and CO\textsubscript{2} emission intensity in basidiocarps gas exchange of bracket fungi, one-way ANOVA test.

| Temperature, °C | Daedaleopsis tricolor | Fomitopsis betulina |
|----------------|-----------------------|--------------------|
|                | CO\textsubscript{2}O\textsubscript{2} | C-CO\textsubscript{2} µg g\textsuperscript{-1} h\textsuperscript{-1} | CO\textsubscript{2}:O\textsubscript{2} | C-CO\textsubscript{2} µg g\textsuperscript{-1} h\textsuperscript{-1} |
| 10             | 0.8 (0.03)            | 191 (14.7)         | 0.8 (0.09)       | 445.1 (20.7)          |
| 20             | 0.9 (0.01)            | 445 (13.4)         | 0.8 (0.01)       | 996.5 (22.5)          |
| 30             | 0.9 (0.03)            | 659.4 (15.6)       | 0.8 (0.03)       | 1495.8 (91.9)         |
| 40             | 0.8 (0.03)            | 511.5 (20.7)       | 0.8 (0.07)       | 1029.0 (46.2)         |
| Relevance to temperature | F(3,8) = 3.88, p = 0.05 | F(6,14) = 20.99, p = 0.001 | F(3,8) = 0.22, p = 0.87 | F(6,14) = 20.01, p = 0.001 |

Values are the average from three replicates (±SE).

4. Discussion

Temperature and humidity are climatic factors that affect the quantitative and qualitative parameters of gas exchange in WD. In particular, as noted above, high moisture content of wood and high temperature promote anaerobic conditions [1,4,20]. Thus, in WD gas exchange, both aerobic and anaerobic CO\textsubscript{2} are represented. Therefore, our tasks included assessment of the relationship between CO\textsubscript{2} and O\textsubscript{2} gas exchange and carbon and oxygen balance in WD. The results showed that CO\textsubscript{2} emission and O\textsubscript{2} uptake are physiologically entwined, and their relationship did not change within the range of temperatures from +10 to +40 °C and the range of RM from 40% to 70%. Therefore, the gas exchange in WD decomposed by xylotrophic Basidiomycetes was aerobic within the entire range of temperatures and moisture typical for temperate climate zone.

It was confirmed by carbon-to-oxygen balance that the average CO\textsubscript{2}-to-O\textsubscript{2} ratio was equal to 0.9, being nearly the same as the data by Solovyov [25], who reported a 1:1 CO\textsubscript{2}-to-O\textsubscript{2} ratio for wood decomposed by xylotrophic Basidiomycetes. In case the oxygen is readily available, the CO\textsubscript{2}-to-O\textsubscript{2} ratio mainly depends on molecular entities decomposed in the respiration, being equal to 1.0 for carbohydrates, 0.8 for proteins and 0.7 for fats [43]. The CO\textsubscript{2}-to-O\textsubscript{2} ratio obtained in our research was within the range specific for aerobic respiration process. The presence of an anaerobic component in the gas exchange was limited, and it can be probably identified for a few cases, when the CO\textsubscript{2}-to-O\textsubscript{2} ratio was 1.4–2.1, which is notably beyond the physiological normal for an aerobic process. These occurrences were rarely observed for gas exchange under the RM of 70% and temperature from +20 to +40 °C. These were specific conditions that depressed diffusion of gases (moisture) and enhanced respiration intensity (temperature). Consequently, the presence of anaerobic CO\textsubscript{2} in the gas exchange of WD is more an exception, and its quantity is minor. As we showed earlier [35], occasionally and in small amounts in the gas exchange of WD decomposed by Basidiomycetes fungi CH\textsubscript{4}, a product of strictly anaerobic processes can be present.

The CO\textsubscript{2}-to-O\textsubscript{2} ratio illustrates the type and balance of gas exchange and the output of CO\textsubscript{2} relative to the scale of O\textsubscript{2} uptake, i.e., the conversion of organic carbon into carbon dioxide efficiency. The average value of the ratio (0.9) indicates a high efficiency of conversion: With each unit of oxygen uptaken, 0.9 unit of CO\textsubscript{2} is formed and released. It means that CO\textsubscript{2} to O\textsubscript{2} fluxes for WD decomposed by xylotrophic Basidiomycetes are closely entwined, and they are of the corresponding scale. In our view, decomposition of WD is seen as biological combustion being accompanied with O\textsubscript{2} uptake and CO\textsubscript{2} release, similar to the physical and chemical combustion. So far as the biological combustion entails billions of tonnes of WD, this process becomes a globally significant CO\textsubscript{2} source and a similar scale of O\textsubscript{2} consumer. Thus, it is necessary to reconcile the contribution WD and its decay agents make to carbon-and-oxygen gas exchange of forest ecosystems and the entire control of the composition of the atmosphere.

According to Solovyov, for xylotrophic Basidiomycetes that decompose wood, the ratio of CO\textsubscript{2} emission to O\textsubscript{2} uptake is irrelevant to temperature, fungus species, and its physiological type (white/brown rot fungi) [25]. Our results also showed the lack of
correlation between the balance of carbon-oxygen gas exchange, the efficiency of oxidation conversion, and the species' physiological type of wood decay fungi. Another conclusion made by Solovyov relates to the lack of a relationship of CO$_2$-to-O$_2$ ratio and temperature. It was made based on gas exchange analysis under +17 and +27 °C temperature levels [25]. Our data confirmed that the ratio between CO$_2$ release and O$_2$ uptake did not show any relevance to the temperature range from +10 and +40 °C, which is typical for the moderate latitudes. We did not see any relevance to wood moisture in the range of RM 40% to 70%. In other words, the carbon-to-oxygen balance of WD and the efficiency of their oxidation conversion are relatively stable environmental and physiological parameters that have no link to wood decay fungi species or moisture and temperature ranges, common for temperate latitudes.

Unlike carbon-and-oxygen balance and oxidation conversion efficiency, the gas exchange intensity of woody debris was closely related to climate. Both CO$_2$ emission activity and the intensity of oxygen uptake were the processes, highly sensitive to temperature variability. The average Q$_{10}$ value under the +10 to +30 °C temperature range was appropriately equal to 2.0 for carbon and 1.8 for oxygen gas exchange. The moisture of wood did not affect temperature sensitivity of gas exchange. The latter indicates the independent nature of temperature as a driver of CO$_2$ and O$_2$ gas exchange activity in WD. The literature data [4,7,9,10,12,30] report on the significant variability of Q$_{10}$ parameter from 1.37–3.99 [4] to 4.06 [10]. Our estimates fit well in this range.

In WD, the temperature is the driver that controls and also limits the intensity of CO$_2$ and O$_2$ gas exchange. Their activity was highest at +30 and +40 °C. Chen et al. consider these temperatures optimum for gas exchange [4]. However, they are equivalent to heat shock for the boreal inhabitants, whose life mostly occurs under +15 °C [1]. In our view, the temperature maximum should not be treated as the highest acceptable, rather than the optimum, for CO$_2$-and-O$_2$ gas exchange for WD. With regard to moisture of Betula wood, it is equal to 60–110 C-CO$_2$ µg g$^{-1}$ h$^{-1}$, being 3–5-fold higher than the actual summer temperatures (+10–+20 °C) and moisture (RM 40%) of Mid-Urals pine and birch forests. Therefore, climate warming may result in the highest 3-fold enhancement of CO$_2$ emission intensity of WD under the current moisture level. However, if the moisture rises, the emission enhancement may be 5 times greater than the highest. The scale of O$_2$ will increase accordingly.

The gas exchange intensity of WD is closely and positively related to its moisture. Our data showed that the RM changes within the 40–70%-range caused a 1.8-fold corresponding and directly related change in the level of CO$_2$ intensity and O$_2$ uptake. The result was equally pronounced at +10, +20, +30, and +40 °C. It confirms that the moisture is the environmental driver of gas exchange that is independent of temperature.

The temperature and moisture are independent but interacting drivers. Their strong interactions are noted in the moisture range of 91–320% [10] and 10–160% [44] under both low and high temperatures [3]. Our results showed that the outcome of their interaction depends on the direction of the changes. If the direction is similar, the overall effect on carbon-and-oxygen gas exchange is summarizing. In case of different directions, there is a difference of particular effects. For oppositely directed temperature and moisture trends, the joint effect can stabilize gas exchange intensity when the influence of one driver is fully or partially compensated by the other. We believe that this phenomenon can play a very important role in the control of carbon-and-oxygen exchange intensity in WD. The precipitation is the major source of moistening of wood residues, and it displays an opposite multi-year trend in relation to temperature change, for example, in the Southern Urals [45]. Being highly important for the carbon cycle of forest ecosystems, this phenomenon requires a detailed investigation, especially since there is also some evidence that temperature and moisture trends have no effect on intensity of WD gas exchange [4].

The moisture and temperature are undoubtedly the most important environmental drivers of O$_2$ and CO$_2$ exchange of woody debris. However, they are just the controllers of its intensity. The wood decay Basidiomycetes are the basic condition and the impact factors
that enable physiological process of gas exchange. This is confirmed by proximity (identity) of exchange parameters identified for WD decomposed by Basidiomycetes and their basidiocarps. The latter represent multifunctional biostructures with intensive respiration [46], available for direct measurement, when superposition of effects from other microorganisms can be effectively avoided. The common features of gas exchange of basidiocarps and WD include strong temperature dependence ($Q_{10} = 1.9$), the highest emission intensity under similar temperature levels ($+30 ^\circ C$), positive physiology-level correlation between $O_2$ and $CO_2$ fluxes ($r = 0.98–0.99$), similar ratio of their scales (0.8–0.9), and independence from temperature, species, and physiological type of wood decay fungi. Solovyov also noted an identical $O_2$-and-$CO_2$ volumetric ratio for gas exchange of wood decomposed by xylotrophic Basidiomycetes and their basidiocarps [25].

The close relationship of gas exchange intensity with species of wood decay Basidiomycetes is a confirmation of the role of these fungi as the main prerequisite and the biotic factor of gas exchange in WD. This may be due to both the specific features of the rate of gas exchange of the mycelium and its different biomass in wood. In our opinion, under any environmental conditions, the qualitative and quantitative parameters of $O_2$ and $CO_2$ gas exchange WD primarily depend on composition of Basidiomycetes fungi, whose physiological activity is determined by temperature and moisture. The qualitative and quantitative parameters of $O_2$ and $CO_2$ exchange primarily depend on the composition of xylotrophic Basidiomycetes, whose physiological activity is determined by temperature and moisture. The relationship between the composition of these fungi and the intensity of decomposition and gas exchange of woody debris has been noted by many authors [21–24,33,47].

5. Conclusions

The gas exchange of WD under the range of temperatures and moisture parameters, typical for temperate latitudes, is of an aerobic nature. It includes two physiologically entwined and closely or equally scaled processes: $CO_2$ emission and $O_2$ uptake. This makes the WD not only the globally significant source of $CO_2$, but also an appropriate scale consumer of $O_2$. The carbon-to-oxygen balance and the efficiency of organic carbon oxidation into carbon dioxide are climate-independent features of WD gas exchange. The intensity of exchange is driven by moisture and temperature and is closely related to climatic factors. The combined effect of moisture and temperature on gas exchange intensity can be displayed in its enhancing: weakening, otherwise stabilizing. The respiration of wood decay Basidiomycetes represents the physiological means of $CO_2$ and $O_2$ gas exchange in WD and, in view of the importance of WD as a $CO_2$ source and $O_2$ consumer, they should be treated as gas-controlling organisms of biospheric significance.

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Data Availability Statement: Data are contained within the article.

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Appendix A

Figure A1. The relationship between \( \text{O}_2 \) and \( \text{CO}_2 \) gas exchange fluxes from WD of \textit{Betula} with (a) white (\textit{Fomes fomentarius}) and (b) brown (\textit{Fomitopsis betulina}) rot and the RM of 40\% (I) and 70\% (II); \( R^2 \), coefficient of determination.

Table A1. The carbon-and-oxygen gas exchange of \textit{Betula} WD decomposed by xylotrophic Basidiomycetes.

| Fungi Species, Dry Mass (g)/Volume of the Samples (l) | Moisture 40/65 per Cent | Moisture 70/245 per Cent |
|------------------------------------------------------|--------------------------|--------------------------|
|                                                      | Temperature, °C | Temperature, °C |
|                                                      | 10 20 30 40 | 10 20 30 40 |
| \textit{Daedaleopsis tricolor}, 5.7/0.02            | 0.05/0.11 0.08/0.08 0.24/0.32 0.25/0.34 0.07/0.13 0.16/0.23 0.39/0.45 0.39/0.46 | 0.03/0.07 0.06/0.06 0.20/0.17 0.24/0.34 0.09/0.15 0.22/0.32 0.48/0.61 0.53/0.81 |
| \( \textit{D. tricolor}, 5.0/0.02 \)                 | 0.03/0.03 0.05/0.07 0.18/0.20 0.25/0.31 0.09/0.16 0.16/0.24 0.38/0.28 0.39/0.51 | 0.04/0.09 0.03/0.06 0.20/0.23 0.17/0.21 0.05/0.06 0.12/0.16 0.37/0.28 0.53/0.49 |
| \( \textit{D. tricolor}, 4.7/0.02 \)                 | 0.03/0.05 0.06/0.15 0.16/0.15 0.17/0.23 0.05/0.11 0.21/0.22 0.27/0.55 0.52/0.90 | 0.03/0.04 0.05/0.08 0.14/0.08 0.15/0.09 0.05/0.08 0.15/0.13 0.26/0.20 0.49/0.46 |
| \textit{Fomes fomentarius}, 5.1/0.03                | 0.05/0.08 0.06/0.08 0.20/0.17 0.26/0.37 0.12/0.10 0.22/0.33 0.50/0.31 0.53/0.47 | 0.04/0.09 0.09/0.12 0.26/0.20 0.27/0.42 0.10/0.24 0.21/0.28 0.44/0.54 0.50/0.38 |
| \( \textit{F. fomentarius}, 6.1/0.05 \)              | 0.04/0.07 0.07/0.08 0.23/0.21 0.27/0.36 0.10/0.16 0.21/0.30 0.47/0.59 0.53/0.56 | 0.04/0.06 0.09/0.13 0.20/0.25 0.24/0.25 0.04/0.08 0.21/0.24 0.49/0.36 0.54/0.59 |
| \( \textit{F. fomentarius}, 5.0/0.04 \)              | 0.01/0.02 0.07/0.07 0.09/0.07 0.13/0.13 0.01/0.03 0.04/0.15 0.10/0.08 0.10/0.16 | 0.05/0.03 0.08/0.10 0.11/0.22 0.14/0.21 0.04/0.09 0.06/0.08 0.12/0.16 0.15/0.23 |
| \textit{Fomitopsis betulina}, 8.0/0.03               | 0.03/0.07 0.06/0.09 0.18/0.11 0.19/0.18 0.05/0.08 0.09/0.07 0.24/0.35 0.31/0.39 | 0.06/0.07 0.16/0.16 0.28/0.32 0.24/0.22 0.16/0.09 0.08/0.06 0.31/0.42 0.28/0.38 |
| \( \textit{F. betulina}, 8.7/0.02 \)                  | 0.04/0.06 0.09/0.13 0.20/0.25 0.24/0.25 0.04/0.08 0.21/0.24 0.49/0.36 0.54/0.59 | 0.06/0.07 0.17/0.20 0.28/0.36 0.24/0.38 0.12/0.16 0.16/0.12 0.40/0.46 0.43/0.47 |
| \( \textit{F. betulina}, 7.6/0.02 \)                  | 0.01/0.01 0.03/0.05 0.03/0.09 0.06/0.09 0.01/0.03 0.03/0.03 0.10/0.11 0.17/0.07 | 0.01/0.01 0.02/0.04 0.02/0.02 0.03/0.03 0.01/0.01 0.03/0.01 0.08/0.10 0.14/0.11 |
| \( \textit{H. rutilus}, 5.3/0.02 \)                    | 0.06/0.07 0.15/0.15 0.28/0.36 0.25/0.30 0.07/0.17 0.05/0.03 0.34/0.48 0.28/0.36 | 0.06/0.07 0.17/0.20 0.28/0.36 0.24/0.38 0.12/0.16 0.16/0.12 0.40/0.46 0.43/0.47 |
| \( \textit{H. rutilus}, 3.0/0.02 \)                    | 0.01/0.01 0.02/0.04 0.02/0.02 0.03/0.03 0.01/0.01 0.03/0.01 0.08/0.10 0.14/0.11 | 0.01/0.02 0.04/0.04 0.03/0.05 0.04/0.02 0.01/0.01 0.04/0.03 0.12/0.13 0.19/0.09 |
| \textit{Steccherinum ochraceum}, 3.3/0.02             | 0.11/0.12 0.19/0.20 0.30/0.55 0.49/0.48 0.15/0.20 0.39/0.46 0.71/0.82 0.63/0.98 | 0.11/0.12 0.21/0.23 0.30/0.57 0.50/0.57 0.15/0.22 0.38/0.42 0.75/0.76 0.62/1.04 |
| \( \textit{T. versicolor}, 5.5/0.03 \)                  | 0.14/0.17 0.25/0.34 0.60/0.85 0.75/0.89 0.56/0.99 0.62/0.77 0.82/1.76 1.28/1.72 | 0.11/0.12 0.21/0.23 0.30/0.57 0.50/0.57 0.15/0.22 0.38/0.42 0.75/0.76 0.62/1.04 |

CO\( _2 \) is in the numerator and O\( _2 \) is in the denominator, % l\(^{-1}\) h\(^{-1}\).
Table A2. The correlation of CO\textsubscript{2} emission of Betula WD decomposed by xylotrophic Basidiomycetes with temperature in the range from +10 to +30 \(^\circ\text{C}\) at two levels of wood moisture.

| Fungi Species               | Moisture 40/65 per Sent | Moisture 70/245 per Cent |
|-----------------------------|-------------------------|--------------------------|
|                             | \(r\)                   | \(p\)                    | \(r\)       | \(p\)       |
| Daedaleopsis tricolor       | 0.93                    | 0.000                    | 0.94        | 0.000       |
| Fomes fomentarius           | 0.86                    | 0.003                    | 0.93        | 0.000       |
| Fomitopsis betulina         | 0.91                    | 0.001                    | 0.97        | 0.000       |
| Hapalopilus rutilans        | 0.89                    | 0.001                    | 0.65        | 0.060       |
| Stecherinum ochraceum       | 0.94                    | 0.000                    | 0.93        | 0.000       |
| Stereum hirsutum            | 0.99                    | 0.000                    | 0.78        | 0.014       |
| Trametes pubescens          | 0.74                    | 0.022                    | 0.96        | 0.000       |
| Trametes versicolor         | 0.89                    | 0.001                    | 0.89        | 0.001       |

\(r\), Pearson correlation factor; \(p\), significance level.

Table A3. The average CO\textsubscript{2} emission intensity of Betula WD decomposed by xylotrophic Basidiomycetes in the temperature range from +10 to +40 \(^\circ\text{C}\) at different wood moisture levels, C-CO\textsubscript{2} \(\mu\text{g g}^{-1} \text{h}^{-1}\).

| Fungi Species               | Moisture 40/65 per Cent | Moisture 70/245 per Cent | \(p\) |
|-----------------------------|-------------------------|--------------------------|-------|
| Daedaleopsis tricolor       | 38.8 (7.40)             | 78.4 (12.92)             | 0.014 |
| Fomes fomentarius           | 27.5 (5.14)             | 67.8 (13.67)             | 0.011 |
| Fomitopsis betulina         | 27.9 (5.21)             | 60.5 (9.22)              | 0.005 |
| Hapalopilus rutilans        | 46.5 (7.34)             | 67.4 (19.37)             | 0.325 |
| Stecherinum ochraceum       | 50.2 (8.55)             | 65.0 (13.21)             | 0.358 |
| Stereum hirsutum            | 33.3 (4.45)             | 39.8 (6.45)              | 0.415 |
| Trametes pubescens          | 14.8 (2.35)             | 41.4 (9.85)              | 0.015 |
| Trametes versicolor         | 76.5 (12.22)            | 136.9 (17.77)            | 0.010 |

Values are the mean (±SE); \(p\), significance level (ANOVA).

References
1. Zavarzin, G.A.; Zavarzina, A.G. Xylotrophic and mycophilic bacteria in formation of dystrophic waters. Microbiology 2009, 78, 523–534. [CrossRef]
2. Pachauri, R.K.; Allen, M.R.; Barros, V.R.; Broome, J.; Cramer, W.; Christ, R.; Church, J.A.; Clarke, L.; Dahe, Q.; Dasgupta, P.; et al. Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change; Core Writing Team, Pachauri, R.K., Meyer, L.A., Eds.; IPCC: Geneva, Switzerland, 2015; p. 151.
3. Boddy, L. Carbon dioxide release from decomposing wood: Effect of water content and temperature. Soil Biol. Biochem. 1983, 15, 501–510. [CrossRef]
4. Chen, H.; Harmon, M.E.; Griffiths, R.P.; Hicks, W. Effects of temperature and moisture on carbon respired from decomposing woody roots. For. Ecol. Manag. 2000, 138, 51–64. [CrossRef]
5. Progar, R.A.; Schowalter, T.D.; Freitag, C.M.; Morrell, J.J. Respiration from coarse woody debris as affected by moisture and saprotroph functional diversity in Western Oregon. Oecologia 2000, 124, 426–431. [CrossRef]
6. Chambers, J.Q.; Schimel, J.P.; Nobre, A.D. Respiration from Coarse Wood Litter in Central Amazon Forests. Biogeochemistry 2001, 52, 115–131. [CrossRef]
7. Gough, C.M.; Vogel, C.S.; Kazanski, C.; Nagel, L.; Flower, C.E.; Curtis, P.S. Coarse woody debris and the carbon balance of a north temperate forest. For. Ecol. Manag. 2007, 244, 60–67. [CrossRef]
8. Jomura, M.; Kominami, Y.; Tamai, K.; Miyama, T.; Goto, Y.; Dannoura, M.; Kanazawa, Y. The carbon budget of coarse woody debris in a temperate broad-leaved secondary forest in Japan. Tellus Ser. B Chem. Phys. Meteorol. 2007, 59, 211–222. [CrossRef]
9. Wu, J.; Zhang, X.; Wang, H.; Sun, J.; Guan, D. Respiration of downed logs in an old-growth temperate forest in north-eastern China. Scand. J. For. Res. 2010, 25, 500–506. [CrossRef]
10. Olajuyigbe, S.; Tobin, B.; Nieuwenhuis, M. Temperature and moisture effects on respiration rate of decomposing logs in a Sitka spruce plantation in Ireland. Forestry 2012, 85, 485–496. [CrossRef]
11. Forrester, J.A.; Mladenoff, D.J.; Gower, S.T.; Stoffel, J.L. Interactions of temperature and moisture with respiration from coarse woody debris in experimental forest canopy gaps. For. Ecol. Manag. 2012, 265, 124–132. [CrossRef]
12. Herrmann, S.; Baulhus, J. Effects of moisture, temperature and decomposition stage on respiratory carbon loss from coarse woody debris (CWD) of important European tree species. Scand. J. For. Res. 2013, 28, 346–357. [CrossRef]
13. Yoon, T.K.; Noh, N.J.; Kim, S.; Han, S.; Son, Y. Coarse woody debris respiration of Japanese red pine forests in Korea: Controlling factors and contribution to the ecosystem carbon cycle. Ecol. Res. 2015, 30, 723–734. [CrossRef]
14. Mukhin, V.A.; Voronin, P.Y.; Sukhareva, A.V.; Kuznetsov, V.V. Wood decomposition by fungi in the boreal-humid forest zone under the conditions of climate warming. *Dokl. Biol. Sci.* 2010, 431, 110–112. [CrossRef] [PubMed]

15. Mukhin, V.A.; Diyarova, D.K.; Veselkin, D.V. Moisture content—The factor of the CO₂ emission activity of woody debris. *Lesovedenie* 2015, 3, 208–213. (In Russian)

16. Ivanov, A.V.; Braun, M.; Zamolodchikov, D.G.; Loshakova, S.Y.; Pototskii, O.V. Carbon Emission from the Surface of Coarse Woody Debris in Korean Pine Forests of Southwestern Primorye. *Russ. J. Ecol.* 2018, 49, 275–281. [CrossRef]

17. Gitarskiy, M.L.; Zamolodchikov, D.G.; Mukhin, V.A.; Grabar, V.A.; Diyarova, D.K.; Ivashchenko, A.I. Carbon fluxes from coarse woody debris in southern taiga forests of the Valdai Upland. *Russ. J. Ecol.* 2017, 48, 539–544. [CrossRef]

18. Mukhortova, L.; Pashenova, N.; Meteleva, M.; Krivobokov, L.; Guggenberger, G. Temperature Sensitivity of CO₂ and CH₄ Fluxes from Coarse Woody Debris in Northern Boreal Forests. *Forests* 2021, 12, 624. [CrossRef]

19. Christensen, J.H.; Hewitson, B.; Busuioc, A.; Chen, A.; Gao, X.; Held, I.; Jones, R.; Kolli, R.K.; Kwon, W.-T.; Laprise, R.; et al. Regional climate projections. In *Climate Change 2007: The Physical Science Basis*. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change; Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K.B., Tignor, M., Miller, H.L., Eds.; Cambridge University Press: New York, NY, USA, 2007; pp. 848–940.

20. Barker, J.S. Decomposition of Douglas-fir coarse woody debris in response to differing moisture content and initial heterotrophic colonization. *For. Ecol. Manag.* 2008, 255, 598–604. [CrossRef]

21. Forrester, J.A.; Mladenoff, D.J.; D’Amato, A.W.; Fraver, S.; Lindner, D.L.; Brazee, N.J.; Clayton, M.K.; Gower, S.T. Temporal trends and sources of variation in carbon from coarse woody debris in experimental forest canopy openings. *Oecologia* 2015, 179, 889–900. [CrossRef]

22. Venugopal, P.; Junninen, K.; Linnakoski, R.; Edman, M.; Kouki, J. Climate and wood quality have decayer-specific effects on fungal wood decomposition. *For. Ecol. Manag.* 2016, 360, 341–351. [CrossRef]

23. Venugopal, P.; Junninen, K.; Edman, M.; Kouki, J. Assemblage composition of fungal wood-decay species has a major influence on how climate and wood quality modify decomposition. *FEMS Microbiol. Ecol.* 2017, 93, 1–8. [CrossRef]

24. Edman, M.; Hagos, S.; Carlsson, F. Warming effects on wood decomposition depend on fungal assembly history. *J. Ecol.* 2021, 109, 1919–1930. [CrossRef]

25. Soloviev, V.A. Respiratory Gas Exchange of Wood; LGU: Leningrad, Russia, 1987; p. 300. (In Russian)

26. Käärik, A.A. Decomposition of Wood. In *Biology of Plant Litter Decomposition*; Dickinson, C.H., Pugh, G.J.F., Eds.; Academic Press: New York, NY, USA, 1974; pp. 129–174; ISBN 978-0-12-215001-2.

27. Swift, M.J. The ecology of wood decomposition. In *Science Progress*; Sage Publications, Ltd.: London, UK, 1977; Volume 64, pp. 175–199.

28. Harmon, M.E.; Franklin, J.F.; Swanson, F.J.; Sollins, P.; Gregory, S.V.; Lattin, J.D.; Anderson, N.H.; Cline, S.P.; Aumen, N.G.; Sedell, J.R.; et al. Ecology of Coarse Woody Debris in Temperate Forests. In *In Fungi in Biogeochemical Cycles*; Gadd, G., Ed.; Cambridge University Press: Cambridge, UK, 1996; Volume 15, pp. 133–302.

29. Blanchette, R.A. Delignification by wood-decaying fungi. *Annu. Rev. Phytopathol.* 1991, 29, 381–398. [CrossRef]

30. Mackensen, J.; Bauhus, J.; Webber, E. Decomposition rates of coarse woody debris—a review with particular emphasis on Australian tree species. *Aust. J. Bot.* 2003, 51, 27–37. [CrossRef]

31. Watkinson, S.; Bebber, D.; Darrah, P.; Fricker, M.; Talika, M.; Boddy, L. The role of wood decay fungi in the carbon and nitrogen dynamics of the forest floor. In *In Fungi in Biogeochemical Cycles*; Gadd, G., Ed.; Cambridge University Press: Cambridge, UK, 2006; pp. 151–181. [CrossRef]

32. Boddy, L.; Frankland, J.; van West, P. *Ecology of Saprotrophic Basidiomycetes*, 1st ed.; Academic Press: New York, NY, USA, 2008; p. 386. ISBN 9780123741851.

33. Hu, Z.; Xu, C.; McDowell, N.G.; Johnson, D.J.; Wang, M.; Luo, Y.; Zhou, X.; Huang, Z. Linking microbial community composition to C loss rates during wood decomposition. *Soil Biol. Biochem.* 2017, 104, 108–116. [CrossRef]

34. Tlaskal, V.; Brabcová, V.; Větrovský, T.; Jomura, M.; López-Mondejar, R.; Oliveira Monteiro, L.M.; Saraiva, J.P.; Human, Z.R.; Cjžh, T.; Nunes da Rocha, U.; et al. Complementary Roles of Wood-Inhabiting Fungi and Bacteria Facilitate Deadwood Decomposition. *Msysystems* 2021, 6, e01078-20. [CrossRef] [PubMed]

35. Mukhin, V.A.; Voronin, P.Y. Methane emission during forest wood decomposition. *Dokl. Biol. Sci.* 2007, 413, 159–160. [CrossRef]

36. Lenhart, K.; Bunge, M.; Ratering, S.; Neu, T.R.; Schüttmann, I.; Greule, M.; Kammann, C.; Schnell, S.; Müller, C.; Zorn, H.; et al. Evidence for methane production by saprotrophic fungi. *Nat. Commun.* 2012, 3, 1–8. [CrossRef]

37. Schroll, M.; Keppler, F.; Greule, M.; Eckhardt, C.; Zorn, H.; Lenhart, K. The stable carbon isotope signature of methane produced by saprotrophic fungi. *Biogeosciences* 2020, 17, 3891–3901. [CrossRef]

38. Scheffer, T.C. O₂ requirements for growth of survival of wood-decaying and sapwood-staining fungi. *Can. J. Bot.* 1986, 64, 1957–1963. [CrossRef]

39. Ryvarden, L.; Gilbertson, R.L. *European Polypores. Part 1 ( Abortiporus – Lindneria);* Fungiflora: Oslo, Norway, 1993; pp. 1–387.

40. Ryvarden, L.; Gilbertson, R.L. *European Polypores. Part 2 ( Meripilus – Tyromyces);* Fungiflora: Oslo, Norway, 1994; pp. 388–743.

41. Mycobank Database—Fungal Databases Nomenclature & Species Banks. Available online: http://www.mycobank.org (accessed on 18 June 2021).

42. Yan, E.; Wang, X.; Huang, J. Concept and classification of coarse woody debris in forest ecosystems. *Front. Biol. China* 2006, 1, 76–84. [CrossRef]
43. Romero-Kutzner, V.; Packard, T.T.; Berdalet, E.; Roy, S.O.; Gagné, J.P.; Gómez, M. Respiration quotient variability: Bacterial evidence. *Mar. Ecol. Prog. Ser.* 2015, 519, 47–59. [CrossRef]

44. Wang, C.; Bond-Lamberty, B.; Gower, S.T. Environmental controls on carbon dioxide flux from black spruce coarse woody debris. *Oecologia* 2002, 132, 374–381. [CrossRef] [PubMed]

45. Agafonov, L.I.; Kukarskikh, V.V. Climate changes in the past century and radial increment of pine in the Southern Ural steppe. *Russ. J. Ecol.* 2008, 39, 160–167. [CrossRef]

46. Mukhin, V.A.; Voronin, P.Y.; Ladatko, V.A.; Ivanov, A.N. The oxygenic and cooperative respiration of the wood-decaying Fungus *Fomitopsis pinicola* (Sw.: Fr.) Pers. *Dokl. Biol. Sci.* 2006, 407, 153–154. [CrossRef] [PubMed]

47. Lustenhouwer, N.; Maynard, D.S.; Bradford, M.A.; Lindner, D.L.; Oberle, B.; Zanne, A.E.; Crowther, T.W. A trait-based understanding of wood decomposition by fungi. *Proc. Natl. Acad. Sci. USA* 2020, 117, 11551–11558. [CrossRef] [PubMed]