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The Specific and Total CO₂ Emission Activity of Wood-Decaying Fungi and their Response to Increase in Temperature

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Abstract: CO_2 emission activity of xylotrophic fungi response to an increase in temperature in the range of 10-30 °C on the example of pure dikaryotic cultures of *Fomes fomentarius* s. str., *F. inzengae*, *Fomitopsis betulina*, *F. pinicola*, *Phellinus igniarius* was analyzed. Emission activity was assessed by the difference in CO_2 concentration in 0.5-liter exposure chambers with Petri dishes with mycelium growing on agar at the beginning of exposure and an hour later using a Gasmet DX-4030 FTIR spectrometer (Gasmet Technologies Oy, Finland), error measurements ±50 ppm. Specific ($\mu g\ CO_2/cm^2/h$) and total ($\mu g\ CO_2/h$) emission activity and its relationship with temperature and size (area) of the mycelium were assessed. It has been shown that in the range of 10-30 °C, the specific and total CO_2 emission activity of the mycelium is closely and positively related to temperature. Specific emission, which is an indicator of the respiratory activity of the mycelium, does not depend on its size; its only driver is temperature, the relationship with which is linear: an increase in temperature by 10 °C causes an increase in the specific emission activity of the mycelium by 1.7 times. The total CO_2 emission activity, which is an indicator of the total amount of CO_2 emitted, is directly proportional to the specific emission activity and the size of the mycelium. In the range of 10-30 °C, an increase in temperature causes an almost equal increase in both the specific emission activity of the mycelium (Q_{10} 1.7) and its growth (Q_{10} 1.5) and causes an exponential increase in the total emission of CO_2. This must be taken into account when predicting CO_2 emissions from woody debris under climate change, as it could potentially contribute to accelerating climate change.

Keywords: fungi; Basidiomycota; respiration; CO_2; emission; temperature; climate

1. Introduction

Climate change, its causes and environmental consequences is one of the most discussed problems in ecology, also in works on the ecology of woody debris and its decomposition [1–5]. This is far from accidental, since woody debris is a globally significant natural reservoir of carbon; in Russian forests alone its reserves amount to about 5.5 Gt. This huge mass of woody debris is at various stages of its biological decomposition – a large-scale and specific to forest ecosystems process, during of which in Russian forest annually about 214 Mt C-CO₂ is emitted into the atmosphere. This makes debris the second natural source of carbon dioxide after soil [1,6].

The main role in the decomposition of debris in forests of temperate latitudes is played by xylotrophic fungi – Basidiomycota, Agaricomycetes [7–10]. This is, perhaps, the only group of organisms in the modern biosphere that has a unique set of interconnected ecological and physiological adaptations to the woody habitat and is capable of decomposing the lignocellulosic complex of wood [11]. They determine the main parameters of CO₂ emission activity of woody debris and this makes them one of the globally significant regulators of the gas composition of the atmosphere [12], factors of climate stability and change [5].

One of the key questions arising from climate change relates to future carbon dynamics, which largely depends on the temperature sensitivity of decomposition processes. They play an important role in the global carbon cycle and, through feedbacks, can potentially influence climate change

[5,13,14]. All currently available data clearly indicate a close connection between the CO_2 emission activity of xylotrophic fungi, wood debris and temperature [3–5,15–21]. In particular, in one of our recent works [22], we showed that an increase in temperature from 20 to 30 °C has a non-additive, possibly synergistic effect on the CO_2 emission activity of xylotrophic fungi, causing its exponential growth.

Considering the role of xylotrophic fungi as factors of stability and climate change, this phenomenon undoubtedly requires its most careful study and, above all, this concerns the temperature response of CO_2 emission activity of xylotrophic fungi to an increase in temperature. This determined the purpose of this work – analysis of the relationships between the CO_2 emission activity of xylotrophic fungi and temperature, testing the hypothesis of an exponential increase in CO_2 emission with increasing temperature in the range of 10-30 °C, which is relevant for temperate latitudes.

2. Materials and Methods

The study of the temperature response of CO_2 emission activity dikaryotic mycelium of five species xylotrophic fungi growth on wort agar was carried out: *Fomes fomentarius* (L.) Fr., *F. inzengae* (Ces. & De Not.) Cooke, *Fomitopsis betulina* (Bull.) B.K. Cui, M. L. Han & Y.C. Dai, *F. pinicola* (Sw.) P. Karst., *Phellinus igniarius* (L.) Quél (Figure 1). Dikaryotic cultures were isolated from basidiocarps of the corresponding species of the fungi using traditional methods [23] and wort (4%) – agar (2%) as a nutrient medium (MA). Use of pure fungi cultures allow to solve of one most difficult problem in the study of xylotrophic fungi – the assessment of mycelium biomass in wood. When mycelium develops on artificial nutrient media, an indicator of its biomass can be such an easily assessed characteristic as the area it occupies in Petri dishes.
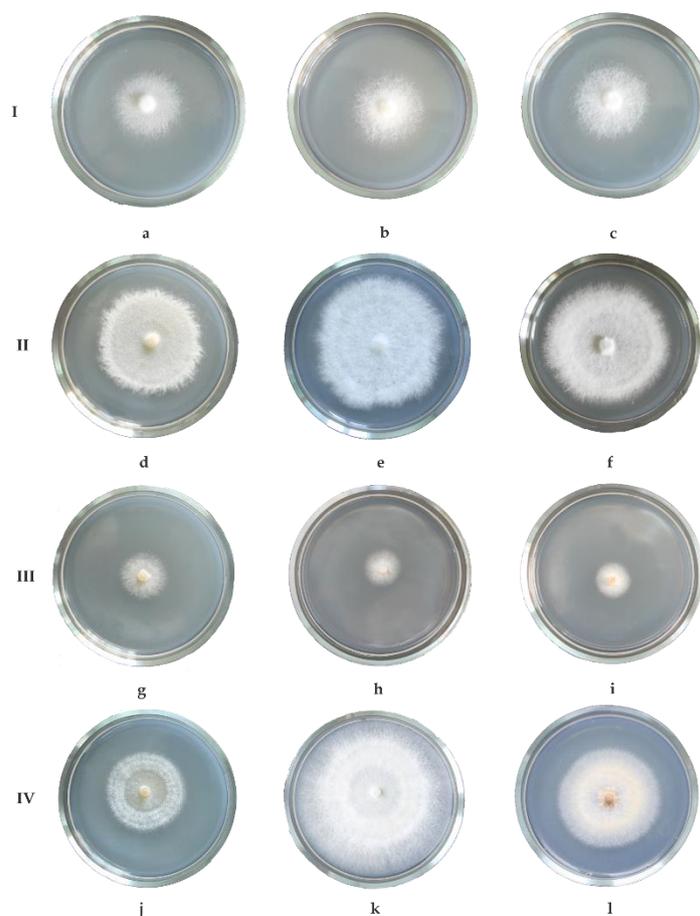

Figure 1. Dikaryotic mycelium of *Fomitopsis betulina* (a, d) *F. pinicola* collected on *Betula* (b, e) and *Picea* (c, f), *Phellinus igniarius* (g, j), *Fomes fomentarius* (h, k) and *Fomes inzengae* (i, l) at the beginning of the experiment (I, III) and after five days (II, IV).

The species identification of basidiocarps was determined on anatomical and morphological characteristics [24], and their species names are given according to Index Fungorum [25]. *F. fomentarius* strains were typed using ITS region sequencing; according to phylogenetic analysis, strains collected on *Populus* L. belong to *F. inzengae*, and on *Betula* L. belong to *F. fomentarius* sensu stricto – to two cryptic taxa [26–28].

The analysis scheme was as follows. Petri dishes (9 cm in diameter, 3 for each strain) were inoculated with a piece of agar (about 5 mm) with the mycelium of the fungus being studied and kept for several days at +25 °C. When the mycelium began to grow around the inoculum, its border was marked by felt-tip pen on the underside of the Petri dishes and dishes were placed in open exposure chambers with a volume of 0.5 l and placed in a thermostat at +10 °C for 2 hours. Then the chambers were sealed, their CO_2 content was measured and placed in a thermostat at +10 °C for one hour. At the end of the exposure, CO_2 measurements in the chambers again were made, after which they were opened and left with closed Petri dishes inside for a day in a thermostat at +10 °C. After 24 hours, the size of the mycelium in Petri dishes was measured and its border was marked, the chambers were closed, CO_2 was measured in them and placed in a thermostat at +10 °C for an hour. At the end of the exposure, the CO_2 content in the chambers was measured again. According to the same scheme, growth of mycelium and its emission activity were assessed at +20 °C, +25 °C, +30 °C and +35 °C.

The CO_2 content in the chambers was measured using a Gasmet DX-4030 FTIR spectrometer (Gasmet Technologies Oy, Finland) with an accuracy of ±50 ppm. The emission activity of the mycelium was assessed by the difference in CO_2 concentration in the chambers at the beginning of the exposure and at it end and was calculated in μg of CO_2, taking into account the volume of the exposure chambers and Petri dishes, exposure duration.

Specific CO_2 emission was calculated in μg $CO_2/cm^2/h$ by equation (1):

$$SEA = \Delta CO_2 \times (V_1 - V_2) / Vm \times M / S \times 0.27 \times 273/T, \tag{1}$$

The total CO_2 emission, or the total amount of carbon dioxide emitted by the mycelium, was calculated in μg CO_2/h by equation (2):

$$TEA = \Delta CO_2 \times (V_1 - V_2) / Vm \times M \times 0.27 \times 273/T, \tag{2}$$

where SEA is the specific CO_2 emission, TEA is the total CO_2 emission, ΔCO_2 is the amount of CO_2 released by the mycelium during exposure (ppm/h), V_1 is the chamber volume (l), V_2 is the sample volume (l), Vm is the molar volume (22.4 l/mol), M – molar mass of CO_2 (44 g/mol), S – area occupied by mycelium (cm^2), T – temperature in Kelvin (K).

The temperature coefficient (Q_{10}) of specific CO_2 emission, showing the multiplicity of its change with a temperature increase of 10 °C, was calculated by equation (3):

$$Q_{10}SEA = SEA_1/SEA_2, \tag{3}$$

where $Q_{10}SEA$ is the temperature coefficient of specific emission, SEA_1 is the specific emission at 10 and 20 °C, and SEA_2 at 20 and 30 °C, respectively.

The temperature dependence of mycelium growth was assessed by the increase in the area it occupied on MA during the day (cm^2/day) and by the temperature coefficient (Q_{10}) of growth calculated by similar equation (4):

$$Q_{10}SM = V_2/V_1, \tag{4}$$

where $Q_{10}SM$ is the temperature coefficient of growth, V_1 is the intensity of mycelium growth (cm^2/day) at 10 and 20 °C, and V_2 is the intensity of mycelium growth at 20 and 30 °C, respectively.

Statistical data processing was performed using the Statistica 10.0 program (StatSoft Inc., USA). Arithmetic means (*m*) are given with standard errors (*SE*). The Pearson correlation coefficient (*r*) was used to characterize the relationships between variables. Student's t-test was used for pairwise comparisons; one-way analysis of variance (ANOVA) was used for multiple comparisons of means. When describing the results of statistical evaluation, the values of the corresponding criteria and its significance are given.

3. Results

Figure 2 shows the dynamics of CO_2 emission activity of five species dikaryotic mycelium at MA in the range of 10-30 °C. It can be seen that the temperature dynamics of total (TEA) and specific (SEA) CO_2 emission activity are significantly different: SEA is linear (determination coefficient 0.91-0.98), TEA is exponential (determination coefficient 0.94-0.99).
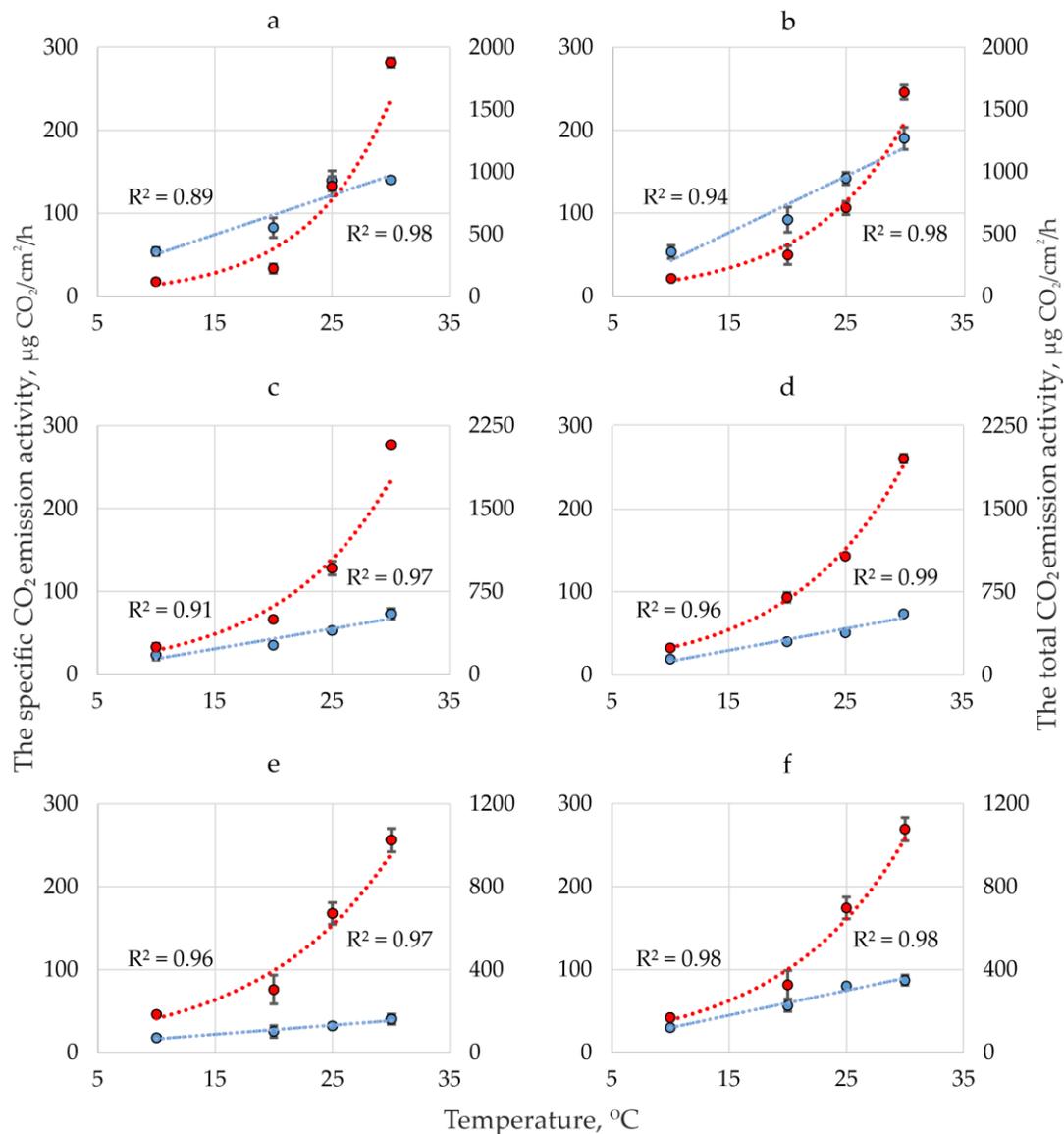

Figure 2. Dynamics of specific (blue, the approximation confidence value on the left) and total (red, approximation confidence value on the right) CO_2 emission activity (m ± SE) of dikaryotic mycelium at MA in the range of 10-30 °C of *Fomes fomentarius* sensu stricto (a), *F. inzengae* (b), *Fomitopsis pinicola* (collected on *Betula*) (c), *Fomitopsis pinicola* (collected on *Picea*) (d), *Fomitopsis betulina* (e) and *Phellinus nigricans* (f).

The Tables 1–3 shows that the temperature rise from 10 to 20 °C increase the specific CO_2 emission activity mycelium from 1.3 (*F. betulina*) to 2.1 (*F pinicola*, collected on *Picea*), on average 1.8 times. An increase in temperature from 20 to 30 °C enhances SEA by 1.2 (*F. fomentarius* s. str.) – 1.9 (*F. pinicola*, collected on *Picea*), on average 1.6 times. In other words, the temperature coefficient of the specific CO_2 emission activity of the mycelium of the studied group of xylotrophic fungi ranges from 1.6 to 1.8. An increase in temperature from 10 to 30 °C (3 times) causes a corresponding increasing in SEA – 2.9 times. At 35 °C, SEA decreases in some of the analyzed fungi, while in *F. betulina* and *F pinicola* (collected on *Betula*) it remains at the same level as at 30 °C.

Table 1. The total and specific CO_2 emission activity of the dikaryotic mycelium of *Fomitopsis betulina* / *Phellinus igniarius* and their relationship with its area and temperature.

Temperature, °C	Mycelium area, cm²	Emission	
		Total, µg CO_2/h	Specific, µg CO_2/cm²/h
10	10±0.5 / 6±0.2	182±5.0 / 168±12.0	18±0.8 / 30±2.8
	*13±1.4 / 6±0.2	233±1.1 /165±47.1	19±2.0 / 30±8.7
20	13±1.4 / 6±0.2	303±69.2 / 326±21.9	25±7.1 / 56±4.3
	*21±1.6 / 9±0.5	490±10.2 / 517±11.2	24±2.2 / 60±4.9
25	21±1.6 / 9±0.5	671±52.5 / 697±20.1	32±2.6 / 80±2.7
	*27±3.0 / 13±0.8	789±34.7 / 988±46.8	30±2.6 /80±5.2
30	27±3.0 / 13±0.8	1024±56.4 / 1077±16.9	40±6.0 / 87±7.3
	*35±3.9 / 18±0.6	1076±87.3 /1062±49.6	33±5.9 / 60±4.7
35	35±3.9 / 18±0.6	1049±129.5 / 946±92.8	32±6.8 / 53±4.2
	*35±3.1 / 19±0.5	917±27.4 / 645±24.7	27±2.4 / 35±0.4

Note: * – here and further in the tables the area of mycelium after 24 hours.

The specific CO_2 emission activity of the mycelium does not show any relationship connection with its size, in our case, with its area. Thus in *F. betulina* strain at 10 °C SEA of the same level (18-19 µg CO_2/cm²/h) for mycelium with an area of 10 and 13 cm², and at 20 °C it is equal 24-25 µg CO_2/cm²/h for mycelium with an area of 13 and 21 cm² (Table 1). In *F. pinicola* (strain collected on *Picea*) at 10 °C, SEA equal to 19 µg CO_2/cm²/h is recorded in mycelium with an area of 11 and 14 cm², and in the strain collected on *Betula* 23 µg CO_2/cm²/h in mycelium of 13 and 18 cm². The same is observed at 30 °C: in the strain collected on *Betula*, the mycelium of 29 cm² and 38 cm² has SEA equal to 73 µg CO_2/cm²/h, and in the strain collected on *Picea* 73-74 µg CO_2/cm²/h in the mycelium with an area of 27 cm² and 35 cm² (Table 2). There is also no relationship between SEA and mycelium area in the *F. fomentarius* s. str. and *F. inzengae* strains (Table 3).

Table 2. The total and specific CO_2 emission activity of the dikaryotic mycelium of *Fomitopsis pinicola* (collected on *Betula* / *Picea*), and their relationship with its area and temperature.

Temperature, °C	Mycelium area, cm²	Emission	
		Total, µg CO_2/h	Specific, µg CO_2/cm²/h
10	11±1.3 / 13±0.8	244±34.7 / 242±17.6	23±6.0 / 19±0.5
	*14±1.3 / 18±1.2	319±20.4 / 336±22.4	23±3.7 / 19±2.5
20	14±1.3 / 18±1.2	495±22.8 / 699±44.7	35±1.7 / 40±2.9
	*18±1.8 / 21±1.4	740±36.9 / 856±0.6	41±4.3 / 40±2.5
25	18±1.8 / 21±1.4	959±62.3 / 1072±18.5	52±2.2 / 50±2.7
	*29±2.3 / 27±1.3	1698±22.0 / 1416±26.6	59±4.4 / 53±2.3
30	29±2.3 / 27±1.3	2076±13.1 / 1955±37.7	73±6.4 / 73±2.6
	*38±2.5 / 35±1.4	2736±44.3 / 2551±35.0	73±6.5 / 74±3.5
35	38±2.5 / 35±1.4	2771±34.1 / 2382±49.2	74±5.7 / 69±1.6
	*42±2.3 / 43±0.9	2670±83.9 / 2290±33.7	65±5.2 / 53±1.2

Table 3. The total and specific CO_2 emission activity of the dikaryotic mycelium of *Fomes fomentarius* sensu stricto / *Fomes inzengae* and their relationship with its area and temperature.

Temperature, °C	Mycelium area, cm²	Emission	
		Total, µg CO_2/h	Specific, µg CO_2/cm²/h
10	2±0.1 / 3±0.2	116±1.1 / 141±15.2	54±4.7 / 53±7.8
	*3±0.1 / 4±0.5	147±17.5 / 250±42.4	55±7.8 / 69±3.6

20	3±0.1 / 4±0.5	222±36.3 / 328±75.4	83±11.9 / 92±15.2
	*6±0.2 / 5±0.5	681±98.0 / 516±13.7	106±11.8 / 104±7.5
25	6±0.2 / 5±0.5	884±78.6 / 707±53.2	139±12.0 / 142±7.4
	*13±0.2 / 9±0.7	2064±133.9 / 1269±98.9	154±9.2 / 146±2.7
30	13±0.2 / 9±0.7	1878±36.9 / 1637±56.9	140±3.0 / 190±13.4
	*19±0.8 / 12±0.8	2401±41.0 / 1868±26.2	127±3.0 / 155±8.2
35	19±0.8 / 12±0.8	2588±127.5 / 1777±82.6	137±1.3 / 147±6.6
	*25±1.3 / 16±1.0	2042±183.5 / 1650±78.9	84±10.7 / 102±10.5

The specific CO_2 emission activity depends on the species of fungus and in the range 10-20 °C, its average value varies from 27.5±1.95 (*F. betulina*) to 118.8±9.53 µg CO_2/cm^2/h (*F. inzengae*). In *F. betulina*, *F. pinicola* it is significantly – $F_{(1, 142)}$ = 90.160, p = 0.001 – lower (varies from 27.5±1.95 to 47.4±4.19, on average 40.3±2.32 µg CO_2/cm^2/h) than in *F. fomentarius* s. str. and *Ph. igniarius* (varies from 60.1±4.59 to 118.8±9.53, on average 95.4±5.31 µg CO_2/cm^2/h). At the same time, *F. pinicola* strains isolated from basidiocarps collected on *Betula* and *Picea* have SEA of the same level (Table 2).

The response of total CO_2 emission activity to an increase in temperature is more pronounced than in the case of specific activity. If, with an increase in temperature from 10 to 20 °C, SEA, as noted, increases by 1.3-2.1 times, on average 1.8 times only, then TEA increases by 3 (*F. betulina*) – 6 (*F. fomentarius* s. str.) times, on average 4 times. When the temperature increases from 20 to 30 °C, TEA increases by 2 (*F. betulina*) – 4 (*F. fomentarius* s. str., *F. pinicola*), on average 3 times, while SEA 1.6 times. An increase in temperature from 10 to 30 °C enhances the TEA of the mycelium of *F. betulina* and *Ph. igniarius* by 6, *F. pinicola* by 10, *F. inzengae* by 13 and *F. fomentarius* s. str. by 21 times – on average 11 times. At the same time, as noted above, SEA will increase by 2.9 times. Like SEA, TEA reaches its maximum at 30 °C; at 35 °C it decreases or remains at the same level as at 30 °C. TEA varies depending on the fungus species: the highest (2000-3000 µg CO_2/h) in the mycelium of *F. fomentarius* s. str., *F. inzengae*, *F. pinicola* and 2-3 times lower (does not exceed 1000 µg CO_2/h) in the mycelium *F. betulina* and *Ph. igniarius* (Table 1, 2, 3).

The total emission activity of the mycelium depends not only on temperature, but also on its size. For example, at 20 °C, an increase in the mycelium area of *F. betulina* by 1.6 times (from 13 to 21 cm^2) is accompanied by a similar 1.6-fold increase in TEA (from 303 to 490 µg CO_2/h). Increase in mycelium size *Ph. igniarius* by 1.5 times (from 6 to 9 cm^2) at 20 °C leads to an increase in its TEA by 1.6 times (Table 1). In *F. pinicola* at 20 °C, an increase in the size of the mycelium by 1.2-1.3 times is accompanied by an increase in *TEA* by 1.2-1.5 times (Table 2). An increase in TEA proportional to the increase in mycelium area is also observed in the *F. fomentarius* s. str. and *F. inzengae* strains (Table 3).

The size of the mycelium reflects the intensity of its growth, which is positively related to temperature. The correlation coefficient of the daily increase in mycelium area with temperature for *F. betulina* is 0.61, *F. pinicola* 0.57 (strain collected on *Picea*) – 0.76 (strain collected on *Betula*), *F. inzengae* and *Ph. igniarius* 0.85, *F. fomentarius* s. str. 0.97. The temperature coefficient (Q_{10}) of mycelium growth with an increase in temperature from 10 to 20 °C varies from 1.3 (*F. inzengae*) to 2.0 (*F. fomentarius* s. str.), and on average is 1.5; it has the same average value when the temperature increases from 20 to 30 °C. At 30 °C growth rate of *F. betulina* and *Ph. igniarius* mycelium reaches its maximum, and *F. pinicola*, *F. inzengae*, *F. fomentarius* s. str. – at 35 °C (Tables 1, 2, 3).

4. Discussion

There is an opinion that for the majority of representatives of the boreal microbiota, adapted to an average summer temperature of about +15 °C, an increase in temperature to 30 °C will be tantamount to temperature shock [6]. However, as the results of this study show, in the range of 10-30 °C, xylotrophic fungi respond positively to increased temperature. Thus, in this range, the specific CO_2 emission activity of the mycelium, which is an indicator of its respiratory activity, increases on average 1.7 times with an increase in temperature by 10 °C and 3 times with its increase from 10 to 30 °C: 1.7 x 1.7 = 2.9. In other words, the specific CO_2 emission activity of the mycelium of xylotrophic fungi obeys the Van't Hoff rule and this determines the linear nature of its temperature dynamics.

The specific emission activity of the mycelium does not depend on the size of the mycelium and its relationship with temperature is described by the following equation (5):

$$SEA_{T2} = SEA_{T1} \times Q_{10SEA}^{(T2-T1)/10},$$ (5)

where SEA_{T1} and SEA_{T2} are specific CO_2 emission at temperature T_1 and T_2, respectively; Q_{10SEA} – temperature coefficient of specific CO_2 emission activity.

Thus, the only driver of the specific CO_2 emission activity of the mycelium of xylotrophic fungi is temperature, or rather its temperature sensitivity, the indicator of which is the temperature coefficient. The latter, in the range of 10-30 °C, varies depending on the species from 1.2 to 2.1, with an average of 1.7. We also recorded similar Q_{10} values of specific CO_2 emission activity when analyzing the gas exchange of wood residues destroyed by xylotrophic fungi: 2.0-2.1 [12,29]. The close positive relationship between specific emission activity and temperature determines its unstable nature; one of the results of this is a fluctuation in the intensity of CO_2 gas exchange of wood residues during the day: an increase in the daytime and a decrease in the night [30].

The total CO_2 emission activity of the mycelium is determined by its specific emission activity and size. Accordingly, its temperature dynamics has two drivers: temperature sensitivity of a) specific emission and b) mycelium growth, indicators of which are the temperature coefficients of specific emission and mycelium growth. The relationship between total emission and temperature is described by the following equation (6):

$$TEA_{T2} = TEA_{T1} \times Q_{10SEA}^{(T2-T1)/10} \times Q_{10SM}^{(T2-T1)/10},$$ (6)

where TEA_{T2} and TEA_{T1} are the total CO_2 emission at temperature T_1 and T_2, respectively; Q_{10SEA} and Q_{10SM} are the temperature coefficient of specific CO_2 emission and mycelium growth, respectively.

Depending on the species of fungi, the Q_{10} of mycelium growth ranges from 1.3 to 2.0, and on average it is 1.5 and the almost identical Q_{10} of specific emission − 1.7. Therefore, an increase in temperature in the range of 10-30 °C causes an almost equal increase in two unidirectional processes – specific CO_2 emission activity and mycelium growth. Their joint action causes an exponential increase in total CO_2 emissions. The dependence on the mycelium size determines another very important feature of the total CO_2 emission activity of xylotrophic fungi. Due to the fact that the growth of mycelium is an irreversible increase in its size and mass, the temperature dynamics of the total emission also has the character of a directed, irreversible process. The total emission reaches its maximum at 30-35 °C, a temperature at which both the maximum specific CO_2 emission activity and the size of the mycelium are observed.

5. Conclusions

In the range of summer temperatures (10-30 °C) that are relevant for temperate latitudes, the CO_2 emission activity of xylotrophic fungi is closely and positively related to temperature. Their specific CO_2 emission activity determined by the respiratory activity of the mycelium and does not depend on its size. The only driver of specific emissions is temperature, an increase in which causes its proportional (linear) increase. The total CO_2 emission activity, which is an indicator of the amount of CO_2 emitted, depends on the size and specific emission activity of the mycelium. It has the character of an irreversible, directional process that increases exponentially with increasing temperature to 30-35 °C. This gives fairly strong grounds to assume that climate warming will lead to an exponential increase in the CO_2 emission activity of woody debris, which, in turn, could potentially contribute to the acceleration of climate change.

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