
GEOGRAPHY

Latitudinal Patterns of the Early Stages of Woody Debris Decay in the Forest Zone of West Siberia

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Abstract—A large data set (sample size >4000) of the decomposition rates of coarse woody debris was collected in field mass loss experiments along the macro-regional profile crossing the entire forest zone of the West Siberian plain (Russia). The profile passed through the entire latitudinal variety of boreal forest ecosystems from forest tundra in the North (67°) to forest steppe in the South (55°). The latitudinal pattern of the initial stage (3–11 yr) of woody debris decay is established, and the relative contribution of environmental factors and substrate quality to the decomposition rate is assessed. The data presented have no analogues in Russia or abroad either by volume or by the geographic coverage.

Keywords: boreal forest ecosystems, woody debris, decomposition, rate, environmental factors, meridional gradient, Western Siberia

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The presence of a huge mass of slowly decomposing wood in forest ecosystems largely determines the characteristic rates of the cycles of carbon and other nutrients in the terrestrial part of the biosphere [1, 2]. Their mobilization and return to the cycle is achieved, first of all, due to the biological decomposition of woody debris (WD) by fungi and microflora. Nevertheless, many aspects of this biosphere-related process are still poorly understood [3–6], which complicates accurate assessment of the effect of heterotrophic respiration and the net balance of the forest, in particular, boreal ecosystems, on climate change. Special attention, according to experts, should be given to accurate assessment of the decomposition rate of woody debris and to identifying its quantitative and qualitative relations with external and internal factors on various spatial and temporal scales [2, 4].

The period of observations and field work, 1977–1990, refers to the latest and most rapid stage of modern global warming in both Russia and the world [9, 10]. The data set was collected along the meridian profile, passing through the forested part of the West Siberian Plain. It includes more than 4000 single observations

of the decomposition rate of seven tree species in 17 regions from the forest–tundra at the northern border of the forest (67°6' N, 71°28' E) to the forest–steppe in the south (55°24' N, 65°26' E). To study the initial stages of WD decomposition, wood samples of the main forest-forming species were placed in the litter. Samples 20 cm in length and 1–3 cm in diameter were prepared from living branches of hardwood (*Betula pubescens* L., *B. pendula* Roth., *Duschekia fruticosa* (Rupr.) Pouzar) and coniferous (*Larix sibirica* Ledeb., *Picea obovata* L., *Pinus sylvestris* L., *P. sibirica* DuRoi) species directly in the areas of their growth. In each region, 70 samples of each species were prepared, weighed in the wet state, measured, marked, and laid out on the litter. The exposure of individual samples ranged from 2.7 to 10.8 years. Additionally, 15 samples of each species were used for determining the dry weight: their wet weight was measured in the field, after that, in the laboratory they were dried at 105°C for 72 hours and then weighed; hence, the proportion of absolutely dry matter was calculated. The rate of WD decomposition was estimated from the mass loss during the exposure period.

Statistical analysis of the results was carried out using the package PRIMER V.7 (PRIMER-E Ltd), MS Excel, and IBM SPSS Statistics v.20. The entire data set was processed by means of nonparametric stepwise multiple regression analysis of the similarity matrices (DistLM: Distance based linear modeling) using the PRIMER V.7 package (PRIMER-E Ltd). A

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peculiarity of the DistLM method is that it can be used to analyze models that contain both qualitative and quantitative independent variables. It is therefore a significantly more powerful statistical tool compared to conventional regression analysis [7]. In particular, it allows for an assessment of the relative contribution of individual independent factors in various model ensembles. The calculation problem was reduced to 1000-fold regression analysis performed on randomized data arrays with a dimension of 6327903 replications for 49 factors (taking into account the binary coding of qualitative variables). The rate of dry weight loss of wood samples (% per year) was regarded as a dependent variable, while the geographical subzone (7; ZONE: forest–tundra, near-tundra woodlands, northern, middle and southern taiga, subtaiga, forest–steppe); type of forest ecosystem (17; FOREST: e.g., spruce forest); type of forest by dominant tree species (7; TREE: e.g., fir); the dominant group of plant species in the understorey (4; SPECLOW: green moss, lichens, grass, shrubs); felling (2; CUT: yes/no); biotope dominated by hardwood/conifers (2; CONLEAF); WD species (5; SUBSTRATE: *B. pubescens*, *B. pendula*, *L. sibirica*, *P. obovata*, *P. sibirica*, *P. sylvestris*); WD being conifer/hardwood (2; SPECONLEAF) were considered as independent qualitative variables. We also assumed the latitude (LAT); duration of sample exposure (EXPO); calendar day of the start of exposure (JD); calendar year of the middle of the observation interval (YEAR); and the initial absolutely dry mass of the samples (MASS) to be independent quantitative variables.

The results of the DistLM analysis are given in Tables 1 and 2. Due to the large sample size, almost all independent variables (except for JD) were significant. The average rate of weight loss throughout the database was $5.81 \pm 0.05\%$ per year, and the median was 5.44 ($n = 3561$, range 0.1–21.95% per year) for the exposure period from 2.7 to 10.8 years (median, 3.8). In addition, the decomposition rate in the first 2.7–3.8 years was higher than in subsequent years (t -test, $6.09 > 5.49\%$ per year, $p < 0.0001$), and the decomposition rate of hardwood WD was higher than that of conifers (t -test, $6.17 > 5.66\%$ per year, $p < 0.0001$), which corresponds to the published data [4]. The differences in the initial sample weights were small (dry weight of 32.9 ± 0.23 g, $n = 3561$), which was predetermined by their initially equal length, leaving only a diameter-related difference and wood density. However, the MASS is at the end of the list of the most significant variables in Table 1, explaining 0.4% of the total variance ($r_p = -0.1$, $p < 0.01$). This corresponds to the significance and direction of the feedback of the WD diameter with the decomposition, which is well known as one of the predictors of the decomposition rate [4]. Despite the brevity of the total observation period (13 years), the calendar year turned out to be positively related to the decomposition rate ($r_p = 0.14$, $p < 0.01$), which can be considered as the effect of the

progressive warming observed during this period in Western Siberia [10], since the temperature of the environment is also one of the most important predictors of wood decay [8].

As shown by the analysis of separate factors of the decomposition rate in the taiga zone (Table 1), the type of forest ecosystem (FOREST), geographical subzone (ZONE), species of wood debris (SUBSTRATE), the type of forest according to the dominant species (TREE), and latitude (LAT) have the greatest effect, explaining 20, 15, 14, 10, and 10% of the differences, respectively. All other significant factors individually have an extremely weak (from 0.2 to 5%), although statistically significant, effect due to the large sample size.

The multiple regression analysis carried out for the available material with step-by-step inclusion of significant factors and taking into account their mutual influence (Table 2) showed that the main factors affecting the decomposition rate, according to the optimal solution of the model, are the type of forest ecosystem (FOREST: 20%) and the type of substrate (SUBSTRATE: 8%). The calendar year (YEAR: 2%), latitude (LAT: 1%), and the initial mass (MASS: 0.4%) also have a significant effect. All of these factors together account for 31% of the observed difference. Thus, among the five best predictors of the general regression model, there was no geographical subzone factor (ZONE) and the contribution of latitude (LAT) was minor. This can be explained by the relationship between the predictors, namely the subzone criterion is clearly correlated with the forest type (FOREST) and, somewhat more weakly, with the WD species (SUBSTRATE); they “attract” the explained variability in the framework of the model. Therefore, after their inclusion in the model, the subzone no longer plays a role as a predictor. If we exclude the FOREST variable from the analysis, then the subzone will turn out to produce the major influence. Nevertheless, the final model envisages the latitude, although playing a marginal role. This allows for an assessment of the relative contribution of the zonal type of ecosystem, representing environmental factors (such as air and soil temperature, moistening regime, etc.), and the quality of the decomposed substrate (tree type, diameter of residue, etc.). The resulting ratio is 73 : 27% in favor of environmental factors.

A useful technique for assessing the rate of wood decomposition in various parts of the boreal forest zone is to associate this indicator with one of the quantitative factors considered. As it turned out, a combination of the geographical subzone and latitude is best suited for this, but only if the WD decomposition data obtained for the southern taiga and subtaiga as well as those obtained for forest–tundra and pre-tundra woodlands are grouped into two larger zones. Figure 1 shows that the latitude data, grouped into five zones obtained as a result of the merger, leads to a well-

Table 1. Nonparametric stepwise multiple regression analysis of similarity matrices (DistLM) applied to the entire database on the decomposition rates of wood debris in the forest zone of Western Siberia: the effect of individual independent variables

Independent variables	Pseudo-F	<i>p</i>	% predictable variance	res.df	regr.df
FOREST	58.376	0.001	19.821	3542	16
ZONE	103.23	0.001	14.851	3551	7
SUBSTRATE	144.47	0.001	13.989	3553	5
TREE	63.422	0.001	9.680	3551	7
LAT	380.24	0.001	9.660	3556	2
SPECLOW	57.981	0.001	4.666	3554	4
YEAR	66.282	0.001	1.830	3556	2
EXPO	51.273	0.001	1.421	3556	2
MASS	25.893	0.001	0.723	3556	2
SPECONLEAF	18.922	0.001	0.530	3556	2
CONLEAF	10.523	0.002	0.295	3556	2
CUT	8.0344	0.006	0.225	3556	2
JD	1.7655	0.183	0.050	3556	2

Pseudo-F is the Fisher pseudo-criterion, *p* is the significance level, res.df is the residual number of degrees of freedom, regr.df is the number of degrees of freedom of regression. Variables are indicated in the text. Variables, significant at $p < 0.05$ are highlighted in bold.

Table 2. Step-by-step multiple regression analysis of similarity matrices (DistLM) applied to the entire database on the decomposition rate of wood debris in the forest zone of Western Siberia: a general regression model

Variables of the model	Corrected R^2	Pseudo-F	<i>p</i>	Prop.	Cumul.	res.df	regr.df
+FOREST	0.19482	58.376	0.001	0.19821	0.19821	3542	16
+SUBSTRATE	0.27302	96.257	0.001	7.8692E-2	0.27691	3538	20
+YEAR	0.29194	95.512	0.001	1.9013E-2	0.29592	3537	21
+LAT	0.30046	44.106	0.001	8.6741E-3	0.30459	3536	22
+MASS	0.30447	21.393	0.001	4.1831E-3	0.30878	3535	23
+ZONE	0.30447	No test		6.8435E-15	0.30878	3535	23
+TREE	0.30447	No test		1.7017E-15	0.30878	3535	23
+SPECLOW	0.30447	No test		5.3973E-16	0.30878	3535	23

Pseudo-F, Fisher's pseudo-criterion; *p*, significance level; Prop., proportion of differences predicted by it; Cumul., accumulated % of predictable variance, res.df, residual number of degrees of freedom; regr.df, number of degrees of freedom of regression. Variables are indicated in the text. Variables significant at $p < 0.05$ are highlighted in bold.

defined linear increase in the WD mass loss at a rate of 0.344% for each degree of latitude in the north–south direction. The applicability of this regression is limited by the northern and southern boundaries of the forest distribution in Western Siberia, the WD diameter (1–3 cm), the initial period of decomposition (up to 11 years), and also, probably, the period of the climatic normal of 1960–1990. It also turned out that to assess the decomposition rates of WD, distinguishing the subtaiga or pre-tundra woodlands as separate zones is unnecessary.

A special issue was a comparison of the WD decomposition rates of different types of trees in the

forests where they are common (this includes the majority of the data obtained), and in forests where these species are suppliers of a “alien substrate.” The goal was to test the hypothesis that the wood substrate decomposes faster in the biotope for which it is natural (spruce for spruce forests, pine for pine forest, etc.). The comparison was carried out within the sub-taiga subzone near the town of Talitsa, Sverdlovsk oblast, 56°94' N, 63°66' E, according to the observations of 1976–1987. The total sample size for the forest with a “natural” wood substrate was 279, that for the forest with a “alien” substrate was 551. Three tree edificators occurring in this region which, at the same time, are widespread in the forests of Western Siberia, were used

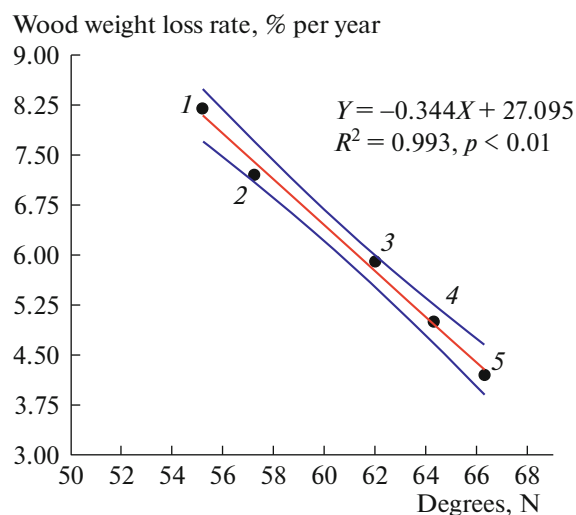


Fig. 1. Dependence of the initial decomposition rate WD (% per year) on latitude (degrees N) in the forest zone of Western Siberia for the years 1977–1990. The average decomposition rates for five geographical subzones (1, forest–steppe; 2, southern taiga, including sub-taiga; 3, middle taiga; 4, northern taiga; 5, forest–tundra), the equation of the linear regression, and the 95% confidence interval are presented. The sample sizes in calculating the average values for individual geographic subzones range from 138 to 1410.

in the comparison: *P. obovata*, *B. pendula*, *P. sylvestris*. Combining three WD species (spruce, birch, pine) and four types of forest (spruce, birch, pine, and aspen) into “species–forest” pairs makes 12 pairs in total.

The average decomposition rate over the entire observation period was slightly greater for the “alien” substrate (5.79% per year > 5.36% per year; *t*-test, *p* = 0.046). It should be noted, however, that the significance of the difference is mostly due to the large sample size, while the difference itself is small (7%). Most likely, with a further increase in the exposure period WD, these values would become similar. At the same time, the difference in the decomposition rate of natural and alien samples is much more significant (Fig. 2). In the first 3–4 years, the WD decomposition rate in “native” biotopes was significantly higher, then in subsequent years it became smaller than in “alien” ones. The predominance of authentic xylotrophic fungi and microflora, adapted to a given substrate in the “native” biotopes and their slow adaptation to a “alien” substrate is the most likely explanation.

The results obtained are the first summarized long-term observations and experiments on the initial stages of decomposition of woody debris in one of the largest forest regions in the world during the most active stage of contemporary warming. In particular, it has been shown with high reliability that the wood weight loss rate linearly depends on the geographical latitude, increasing from north to south; the relative contribu-

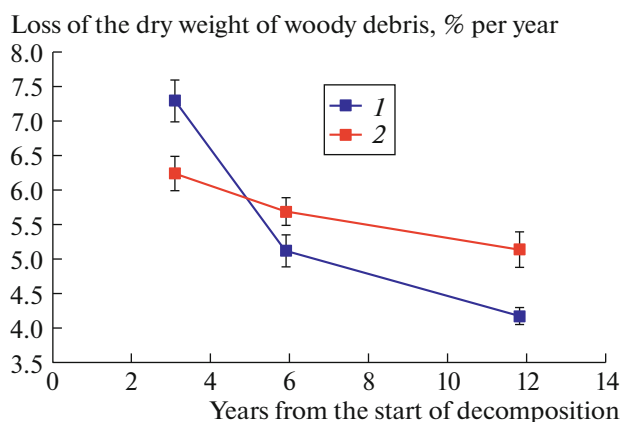


Fig. 2. Comparison of the WD mass loss rate during the initial period of decomposition (2.7–10.8 years) (1) in forest biotopes with predominance of the same tree species, and (2) in biotopes with predominance of other tree species (Sverdlovsk oblast, sub-taiga; 1976–1987). The average values and their standard errors are given. All pairwise differences are significant (*t*-test, *p* < 0.001). The sample sizes of the points on the graph range from 76 to 244. Explanations are given in the text.

tions of the environmental factors and the quality of the wood substrate are 73 and 27%, respectively; the decomposition rate can significantly increase even in relatively short observation intervals (13 years) during the active period of climate warming, and also can vary depending on very small variations (1–3 cm) in the branch diameter; complexes of xylotrophic fungi and the microflora adapted to the decomposition of individual tree species, which is reflected in a greater decay rate compared to the unusual substrate for a given biotope. The quantitative patterns found can be used to adjust and refine macro-regional and biospheric models of the organic matter cycle depending on climate change.

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REFERENCES

1. G. A. Zavarzin, in *Proc. Russ. Acad. Sci. President's Council-Seminar "Possibilities of Prevention of Climate Change and its Negative Implications: The Kyoto Protocol"*

- Problems*" (Nauka, Moscow, 2006), pp. 134–151 [in Russian].
2. V. N. Kudeyarov, G. A. Zavarzin, S. A. Blagodatskii, A. V. Borisov, P. Yu. Voronin, V. A. Demkin, T. S. Demkina, I. V. Evdokimov, D. G. Zamolodchikov, D. V. Karelin, A. S. Komarov, I. N. Kurganova, A. A. Larionova, V. O. Lopes de Gerenyu, A. I. Utkin, and O. G. Chertov, *Carbon Pools and Fluxes in Russian Terrestrial Ecosystems* (Nauka, Moscow, 2007) [in Russian].
 3. V. A. Mukhin, *The Biota of Xylotrophic Basidiomycetes in the Western Siberian Plain* (UIF "Nauka," Yekaterinburg, 1993) [in Russian].
 4. D. V. Karelin and A. I. Utkin, *Lesovedenie*, No. 2, 26–33 (2006).
 5. G. A. Zavarzin and A. G. Zavarzina, *Microbiology* (Moscow) **78** (5), 523–535 (2009).
 6. M. L. Gitarskii, D. G. Zamolodchikov, V. A. Mukhin, D. K. Diyarova, V. A. Grabar, D. V. Karelin, A. I. Ivashchenko, and A. S. Marunich, *Lesovedenie*, No. 3, 239–249 (2020).
 7. M. J. Anderson, R. N. Gorley, and K. R. Clarke, *PERMANOVA+for PRIMER: Guide to Software and Statistical Methods* (PRIMER-E Ltd., Plymouth, 2008).
 8. M. E. Harmon, J. F. Franklin, F. J. Swanson, et al., *Adv. Ecol. Res.* **15**, 133–302 (1986).
 9. *IPCC, 2014: Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II, and III to the 5th Assessment Report of the Intergovernmental Panel on Climate Change*, Ed. by Core Writing Team, R. K. Pachauri, and L. A. Meyer (IPCC, Geneva, 2014).
 10. Climate Features in Russian Federation in 2018. Report. (Rosgidromet, Moscow, 2019). http://www.meteor.ru/upload/pdf_download/o-klimat-rf-2018.pdf.

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