

Application of mathematical models to describe the wood decomposition process caused by lignin-degrading fungi

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Our study used modeling approaches to describe the decomposition of wood and wood constituents caused by lignin-degrading fungi. Several models, which describe wood-mass loss versus time, lignin-mass loss versus wood-mass loss, and lignin-mass loss versus time, were sequentially examined, based on the empirical data obtained for *Trametes pubescens*, *Bjerkandera adusta*, *Ceriporiopsis subvermispora* and *Phanerochaete sanguinea*. We determined that simultaneous white-rot fungi degrade lignin in a linear relationship to wood-mass loss, while lignin degradation caused by successive white-rot fungi corresponds to an exponential dependency. All the parameters of the introduced models were estimated, particularly the 'specific rates of decomposition' and the 'lignin degradation indexes.' The resulting approach provides a method to understand the kinetics of the decomposition of wood constituents caused by wood-inhabiting fungi and allows researchers to perform comparative studies of novel isolates and species. Through the use of models, it was determined that the *P. sanguinea* strain 16–65 causes more selective delignification of *Populus tremula* and *Picea abies* wood than does *C. subvermispora*, and this effect can be promising in biotechnology.

Keywords: biopulping, biodegradation, white-rot, lignin, delignification.

A unique group of xylotrophic fungi that cause white rot of wood are of great interest to science and industry. The fungi are distinguished by their ability to produce extracellular enzymes that are able to degrade lignin, the most recalcitrant natural component in the world (Crawford 1981, Kirk & Farrell 1987, Cullen & Kersten 2004). Because these enzymes affect a wide range of substrates and have the potential to produce high levels of oxidation, they can be used to degrade many forms of organic xenobiotics (polycyclic aromatic hydrocarbons, polychlorinated biphenyls and dioxins, DDT, and many chlorinated phenols) and for the treatment of industrial wastewater (Bezalel *et al.* 1996, Eggen & Majcherczyk 1998, Lamar *et al.* 1999, Raghukumar & Rivonkar 2001). In the timber industry, the lignin-degrading enzymes can be applied to biologically bleach cellulose (Aleksandrova &

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Medvedeva 1999, Jasper *et al.* 1994) and can be used for the production of wood composites (Hüttermann *et al.* 2001, Kadimaliev *et al.* 2001). Wood wastes that have passed through the preliminary fermentation process can be applied for ethanol reception (Kim & Dale 2004, Dashtban *et al.* 2009) and for ruminant feeding (myco-fodder) in agriculture (Schmidt 2006, Alborés *et al.* 2006). Of particular interest is the fungi's ability to selectively destroy lignin while preserving the cellulose component. Application of these microorganisms can essentially change the technological approaches of the pulp and paper industry by substituting highly contaminating treatments with biological and environmentally friendly technologies (Soloviev *et al.* 1985, Soloviev 1986, Kirk *et al.* 1997, Ferraz *et al.* 2008, Singh *et al.* 2010, Liew *et al.* 2011, Yildirim & Yildiz 2011). In this respect, some of these white-rot fungi, such as *Phanerochaete sanguinea* (Fr.) Pouzar and *Ceriporiopsis subvermispora* (Pilát) Gilb. et Ryvarden were intensively studied all over the world (Blanchette 1991, Blanchette *et al.* 1992, Blanchette *et al.* 1998, Soloviev & Jakovleva 1987, Setliff *et al.* 1990).

Analytical methods to quantitatively determine the components of wood are well known and successfully applied. The empirical data obtained from these methods allow researchers to estimate the concentration of the components in analyzed fungi-treated wood samples, but they do not provide all the information about the kinetics of their degradation. Applying these mathematical models allowed us to obtain indexes that can be useful in determining the loss of the mass of the components caused by wood-rotting fungi in any stage or time period of decay and to get a complete set of characteristics for various fungal strains to compare their abilities to degrade wood. The goal of our research is to compare wood and lignin degradability features of successive white rot (*Ceriporiopsis subvermispora*, *Phanerochaete sanguinea*) and simultaneous white rot (*Trametes pubescens* (Schumach.) Pilát, *Bjerkandera adusta* (Willd.) P. Karst.) by employing the suggested mathematical models.

Materials and methods

Fungal cultures and inoculum preparation

Phanerochaete sanguinea 16–65, *Trametes pubescens* 5–08 and *Bjerkandera adusta* 13–07 were obtained from the culture collection of the Department of Ecology, Physiology of Plants, and Wood Science, Saint Petersburg State Forest Technical University (FTU), Russia. *Ceriporiopsis subvermispora* L-14807 SS-3 was provided by the Center for Forest Mycology Research, Forest Product Laboratory (FPL), Department of Agriculture, Madison, USA.

Wood samples preparation

Wood samples (3.0 × 2.0 × 0.5 cm tangential, radial, and cross sections, respectively) were cut from the circumferential part of the sapwood of spruce

(*Picea abies*) and aspen (*Populus tremula*), both approximately 40 years old. To take care of the wood extractives and cell wall components for subsequent fungal degradation experiments, we excluded the changes that occur when heat is applied during oven drying at 103 ± 2 °C and replaced them with the moisture-conditioning method (Schmidt 2006). The samples were placed in a desiccator for three days to reach equilibrium humidity and then weighed. Ten percent of the conditioned specimens (not used in subsequent work) were oven-dried to determine the initial mass of dry wood and the proportion of the wood's moisture content:

$$u = (MC - MD) \times 100/MD \quad (1)$$

where u is the percentage of moisture in the wood sample, MC is the mass (g) of the conditioned sample, and MD is the mass (g) of the dry sample.

The theoretical dry mass of a sample was calculated with the following:

$$MDt = (100 \times MC)/(100 + u_m) \quad (2)$$

where u_m is the mean percentage of moisture in the wood samples, MC is the mass (g) of the conditioned sample, and MDt is the theoretical dry mass (g) of a sample.

The conditioned wood samples were immersed in water for three days and were exposed to fractionated sterilization (tyndallization). The tyndallization protocol requires a daily heating at 100°C for 60 min for three days. This procedure ensures the destruction of the fungal vegetative cells after germination of any spores that survive the heating. The residual water was drained.

Decay test

The fungi were maintained on 2 % (m/v) malt extract (ME) agar in 250 ml Erlenmeyer flasks. After two weeks, when most of the solid media was assimilated by the fungi, spruce or aspen wood chips (size $0.5 \times 0.5 \times 0.5$ cm) were placed over the fungal biomass and incubated until covered with the aerial mycelium, resulting in fungi-treated wood chips.

Glass jars (200 ml each) containing 10 g of vermiculite (0.2–0.5 cm fraction) and 40 ml of 2 % ME were sterilized, chilled, and supplemented with fungi-treated wood chips. Three weeks later, the wood samples, prepared as described above (see Wood samples preparation) were placed into the jars on the surface of a mycelial mat and incubated at 28 °C. Control wood samples were maintained under the same conditions but without a fungal culture (Soloviev & Malysheva 2004).

The samples of successive white rot (*P. sanguinea*, *C. subvermispora*) were weighed after 7, 21, 52, 80, 120, and 196 days of cultivation, and the samples of simultaneous white rot (*B. adusta* and *T. pubescens*) were weighed after 10, 25, 40, 70, and 100 days. Because *B. adusta* and *T. pubescens* are not associated with coniferous wood in the natural environment, the kinetics studies of these species were performed only with aspen specimens. Ten spec-

imens of each wood sample were cleaned of aerial mycelium and oven-dried at 103 ± 2 °C to reach the absolute mass. The percentage of mass loss from the original sample mass, the mean mass loss at every stage of decay, and its standard deviation were calculated. Parameters of the empirical Models 4, 5, 6, 7, 8, and 9, used to describe wood- and lignin-mass losses during fungal degradation, were estimated using Statgraphics Centurion XV software, version 15.2.11, in a nonlinear regression mode.

Lignin determination

Air-dried wood samples were ground in the blender, and the resulting wood meal was sifted through a 1 mm mesh sieve screen. Then, the probes were extracted with diethyl ether in a Soxhlet extractor for 2 hours. For hydrolysis, 500 mg of pre-extracted sawdust was mixed with 5 ml of ice-cold 72 % sulfuric acid and incubated for 2.5 hours at 24 °C while it was stirred constantly. The solution was transferred to a 250 ml measuring flask with 75 ml distilled water and hydrolyzed again with a backflow condenser at 100 °C for an hour. The hydrolysis residue was filtered through the filter paper and determined gravimetrically to be Klason-lignin content. Lignin composition data at various stages of fungal decay were translated into mass losses of lignin from its original mass in sound wood:

$$\delta_L = 100 - (100 - \delta) \times K / K_0 \quad (3)$$

where δ_L is the percentage of lignin-mass loss, δ is the percentage of wood-mass loss, K is the percentage of lignin composition in decayed wood, and K_0 is the percentage of lignin composition in sound wood.

Results

Wood mass loss and decay models

Mass loss is the most commonly used measure to determine the amount of wood decomposition by fungi. *Ceriporiopsis subvermispora* L-14807 SS-3 caused a greater mass loss when compared to *P. sanguinea* 16-65, both in the aspen and spruce wood samples. After 196 days of *P. sanguinea* 16-65 cultivation, the level of decomposition in the spruce samples (38 % mass loss) was higher when compared to that of the aspen samples (23 % mass loss). In contrast, decomposition rates of both aspen and spruce caused by *C. subvermispora* L-14807 SS-3 were similar, reaching 58 % and 54 %, respectively, as shown in Tab. 1.

The most significant mass losses of wood were caused, as expected, by simultaneous white-rot fungi: *B. adusta* 13-07 and *T. pubescens* 5-08. The fungus *T. pubescens* 5-08 induced the greatest mass loss among all the fungal cultures examined. Mass losses produced by simultaneous white-rot fungi during various stages of decay indicate their intensive decomposition ability, as shown in Tab. 2.

After we determined mass losses, we could define the specific rates of decomposition of each wood species caused by successive and simultaneous

Tab. 1. – Wood-mass loss in aspen and spruce samples caused by the successive white-rot fungi *Ceriporiopsis subvermispora* and *Phanerochaete sanguinea*.

Day	<i>C. subvermispora</i> L-14807 SS-3				<i>P. sanguinea</i> 16-65			
	Aspen		Spruce		Aspen		Spruce	
	δ , %	S.E.	δ , %	S.E.	δ , %	S.E.	δ , %	S.E.
7	-0,36	0,41	-0,79	0,45	-0,84	0,13	0,35	0,33
21	2,82	1,47	3,66	0,49	2,00	0,23	0,97	0,56
52	22,33	2,97	11,49	1,97	4,15	0,47	3,91	0,42
80	28,94	3,03	27,46	1,69	8,24	0,84	6,80	1,14
120	40,18	2,24	34,16	1,73	14,63	0,47	7,88	1,37
196	57,60	10,28	54,19	5,01	23,39	3,41	37,95	5,91

Tab. 2. – Wood-mass loss in aspen samples caused by the simultaneous white-rot fungi *Bjerkandera adusta* and *Trametes pubescens*.

Day	<i>B. adusta</i> 13-08 / Aspen		<i>T. pubescens</i> 5-08 / Aspen	
	δ , %	S.E.	δ , %	S.E.
10	0,54	0,83	5,74	1,13
25	14,23	0,80	24,97	1,75
40	24,56	2,63	53,79	1,63
70	55,64	1,83	76,33	1,35
100	77,79	1,57	86,13	1,88

white-rot fungi. To describe kinetic curves of wood decomposition, we used two empirical models (Soloviev & Malysheva 2004):

$$\delta = \delta_{\max} \times (1 - \exp(-k_2 \times t)) \quad (4)$$

$$\delta = \delta_{\max} \times (k_1 \times (1 - \exp(-k_2 \times t)) - k_2 \times (1 - \exp(-k_1 \times t))) / (k_1 - k_2) \quad (5)$$

where δ is the percentage of wood mass loss, δ_{\max} is the percentage of maximum wood mass loss, t is the number of days of degradation, and k_1 and k_2 are the specific rates (day⁻¹) of decomposition.

Decay caused by wood-inhabiting fungi is a multistage process that includes: (1) the initial phase when the colonization by the fungus starts, (2) the latent phase when the substrate is colonized entirely, (3) the regular decay phase when the degradation occurs most actively, and (4) the stationary phase when the resources are exhausted and the fungal development is retarded. Using Model 4, we described the regular decay phase, because it excludes the initial and latent phases. However, the major volume of the mass loss was observed during the regular decay phase and the chosen model reliably describes wood decomposition versus time. Model 4 is universal and can be used to describe all types of wood decay processes (brown rot, white rot, or soft rot). However, Model 5 potentially provides the possibility to estimate the initial and latent phases—the main advantage of the model.

The induction time (t_0) for Model 4 was estimated according to experimental data. In Model 5, induction time was defined according to experimental data or was accepted as equal to zero. The maximum mass loss for all models was estimated according to experimental data or was set equal to 100%. The selection of the appropriate models was determined by the coefficient of determination (R^2) and the positions of points relative to the curve. The most reliable parameters of successive and simultaneous wood decay are presented in Tab. 3.

Tab. 3. – Kinetics of wood decomposition by successive and simultaneous white-rot fungi.

Fungal strain; Tree species	Model N_2^*	t_0 , day	δ_{\max} , %	$k_1 \times 10^{-3}$, day ⁻¹	$k_2 \times 10^{-3}$, day ⁻¹	R_2 , %
<i>Phanerochaete sanguinea</i> 16–65; Aspen	1	14,1	100,0	–	1,4	99,2
	2	–0,3	45,7	24,2	4,8	99,4
<i>Phanerochaete sanguinea</i> 16–65; Spruce	2	0,0	51,3	27,8	3,9	99,4
	1	25,1	100,0	–	2,0	79,8
<i>Ceriporiopsis subvermispora</i> L-14807 SS-3; Aspen	2	0,0	100,0	5,9	5,9	90,2
	1	9,7	83,3	–	6,2	99,2
<i>C. subvermispora</i> L-14807 SS-3; Spruce	2	0,0	79,7	82,6	6,9	99,0
	1	12,0	100,0	–	4,1	98,7
	2	5,1	92,8	71,6	4,9	98,9
<i>Trametes pubescens</i> ; Aspen	2	0,0	87,5	44,7	5,6	98,8
	1	8,4	100,0	–	22,3	98,8
	2	3,8	89,1	53,4	53,4	99,6
<i>Bjerkandera adusta</i> ; Aspen	2	0,0	92,3	45,4	45,5	99,3
	1	12,7	100,0	–	14,2	96,8
	2	5,0	100,0	29,0	29,1	99,6
	2	0,0	100,0	26,5	26,6	99,1

* Models:

$$1. \delta = \delta_{\max} \times (1 - \exp(-k_2 \times t))$$

$$2. \delta = \delta_{\max} \times (k_1 \times (1 - \exp(-k_2 \times t)) - k_2 \times (1 - \exp(-k_1 \times t)) / (k_1 - k_2))$$

Based on the high value of R^2 , we determined that all of the models adequately describe the wood decay process. We found that Model 5, with additional parameters of inductive time (t_0) and maximum mass loss (δ_{\max}), estimated from experimental data, was the most strict and sensitive. This model can be used to provide a detailed description of the multistage decay process.

Empiric models of lignin degradation

The relationship between lignin-mass loss and wood-mass loss caused by simultaneous white rot is characterized by a linear dependency. In this case, lignin degradation can be described by Model 6 (as shown in Fig. 1 a and b):

$$\delta_L = j \times (\delta - \delta_0) \quad (6)$$

where δ_L is the percentage of lignin-mass loss, δ is the percentage of wood-mass loss, δ_0 is the percentage of wood-mass loss when the initial lignin degradation started, and j is the lignin degradation index.

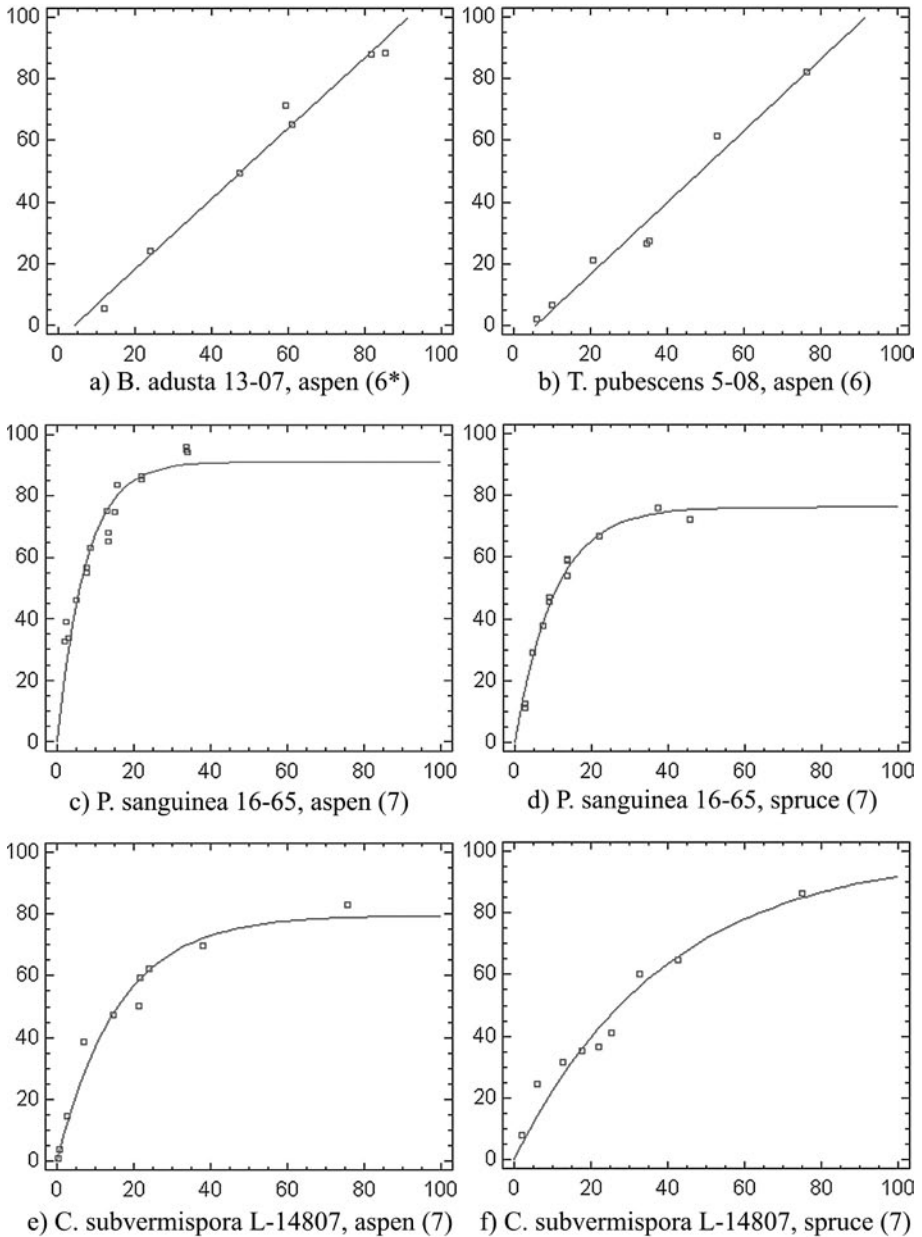


Fig. 1. Lignin mass losses in wood during simultaneous (a, b) and successive (c, d, e, f) white rot at various stages of wood decay: abscissa – wood mass losses, %; ordinate – lignin mass losses, %; * This number corresponds to the mathematical model number in the text.

Tab. 4. – Parameters of the lignin degradation model estimated for simultaneous white-rot fungi.

Tree species/ kinetic model parameters	δ_0 , %	j	R^2	S.E.
<i>Bjerkandera adusta</i> 13–07				
Aspen sapwood / $\delta_{\max} = 100$ %; $k = 14,2 \times 10^{-3} \text{ day}^{-1}$; $t_0 = 12,7$ days	4,3	1,15	98,8	0,027
<i>Trametes pubescens</i> 5–08				
Aspen sapwood / $\delta_{\max} = 100$ %; $k = 22,3 \times 10^{-3} \text{ day}^{-1}$; $t_0 = 8,4$ days	5,8	1,16	96,9	0,054

The point where the linear function crosses the abscissa (δ_0) shows that the degradation of lignin began only after the wood was initially degraded. According to Model 6, *T. pubescens* 5-08 and *B. adusta* 13-07 initiated lignin degradation after causing wood-mass losses of 5.8% and 4.3%, respectively, as shown in Tab. 4. The lignin degradation index (j) resulted from the ratio between lignin-mass loss and wood-mass loss. It should be noted that the main drawback of the linear model is the impossibility to set the maximum lignin-mass loss ($\delta_{L\max}$).

The dependency of lignin degradation on wood-mass loss caused by successive white-rot fungi can be described by exponential Model 7 (Fig. 1 c, d, e and f):

$$\delta_L = \delta_{L\max} \times (1 - \exp(-i \times \delta)) \quad (7)$$

where δ_L is the percentage of lignin mass loss, $\delta_{L\max}$ is the percentage of maximal lignin-mass loss, δ is the percentage of wood-mass loss, and i is the lignin degradation index.

The lignin degradation index (i) characterizes the change of lignin-mass loss with regard to the change of wood-mass loss caused by successive white-rot fungi and is described by a differential function: $i = d\delta_L / d\delta \times \delta_L$. In Model 7, the maximal lignin-mass loss ($\delta_{L\max}$) was established from experimental data, except for the spruce-sample degradation caused by *C. subvermispora* L-14807 SS-3, where $\delta_{L\max}$ was set to 100%, as shown in Tab. 5.

It is incorrect to compare the lignin degradation index (i), estimated with Model 7, with j , which has another mathematical meaning and is estimated with Model 6. As opposed to the specific rates of decomposition (k_1 and k_2), which depend on many factors and changes in a wide range for one fungal strain, lignin decomposition indexes (i and j), estimated for a certain fungal strain and a certain tree species, should be the permanent characteristics.

After we determined indexes i and j , we estimated the lignin decomposition versus time. For this purpose, in Models 6 and 7, we substituted the wood-mass loss parameter by its mathematical equation (Eq. 4) and obtained the dependency of lignin degradation on time:

$$\delta_L = j \times (\delta_{\max} \times (1 - \exp(-k \times (t - t_0))) - \delta_0) \quad (8)$$

$$\delta_L = \delta_{L_{\max}} \times (1 - \exp(-i \times \delta_{\max} \times (1 - \exp(-k \times (t - t_0)))))) \quad (9)$$

Parameters t_0 , δ_{\max} , and k_2 , estimated previously (see *Mass loss of wood and decay models*), were additionally inputted into these models. Thus, the models incorporated the values of time, which was necessary for the establishment of the fungal infection induction of the substrate decomposition. The lignin decomposition, therefore, began at t_0 , which was specific for each fungal strain. Additionally, parameter δ_0 was inputted into Model 8, providing the lag-phase during the initial lignin degradation caused by simultaneous white-rot fungi.

Tab. 5. – Parameters of the lignin degradation model estimated for successive white-rot fungi.

Tree species/ kinetic model parameters	$\delta_{L_{\max}}$, %	$i \times 10^{-2}$	R^2	S.E
<i>Phanerochaete sanguinea</i> 16–65				
Aspen sapwood/ $\delta_{\max} = 100$ %; $k_2 = 1,4 \times 10^{-3}$ day $^{-1}$; $t_0 = 14,1$ days	91,1	13,5	91,3	0,015
Spruce sapwood/ $\delta_{\max} = 100$ %; $k_2 = 2,0 \times 10^{-3}$ day $^{-1}$; $t_0 = 25,1$ days	76,2	9,7	97,6	0,008
<i>Ceriporiopsis subvermispora</i> L-14807 SS-3				
Aspen sapwood/ $\delta_{\max} = 83,3$ %; $k_2 = 6,2 \times 10^{-3}$ day $^{-1}$; $t_0 = 9,7$ days	79,6	6,2	97,2	0,009
Spruce sapwood/ $\delta_{\max} = 100$ %; $k_2 = 4,1 \times 10^{-3}$ day $^{-1}$; $t_0 = 12,0$ days	100,0	2,5	94,9	0,002

From the final modeling results, we determined that simultaneous white-rot fungi, *T. pubescens* and *B. adusta*, degrade lignin faster than successive white-rot fungi, *C. subvermispora* and *P. sanguinea* (see Fig. 2). We assume these results were due to the high speed of total decomposition caused by simultaneous white-rot fungi. The fungus *T. pubescens* was found to be the most efficient lignin degrader from all assayed fungal cultures. According to the obtained data, *C. subvermispora* L-14807 SS-3 started lignin decomposition earlier than any other fungus, and at first provided large amounts of lignin degradation. Nevertheless, the lignin losses caused by *P. sanguinea* 16–65 eventually became higher with time.

Discussion

Differences in the speeds at which successive and simultaneous white-rot fungi decompose wood are dictated by the different enzyme activities and the order of their expression. However, it is considered that lignin degradation is the primary target of the successive white-rot fungi, while simultaneous white-rot fungi degrade lignin with no preference to the other chemical components of wood (Schmidt 2006).

To compare the speeds at which different fungi decay wood, it is more convenient to use an exponential model (Model 4) with a preset inductive time (t_0), because it contains only one parameter, k_2 , characterizing the spe-

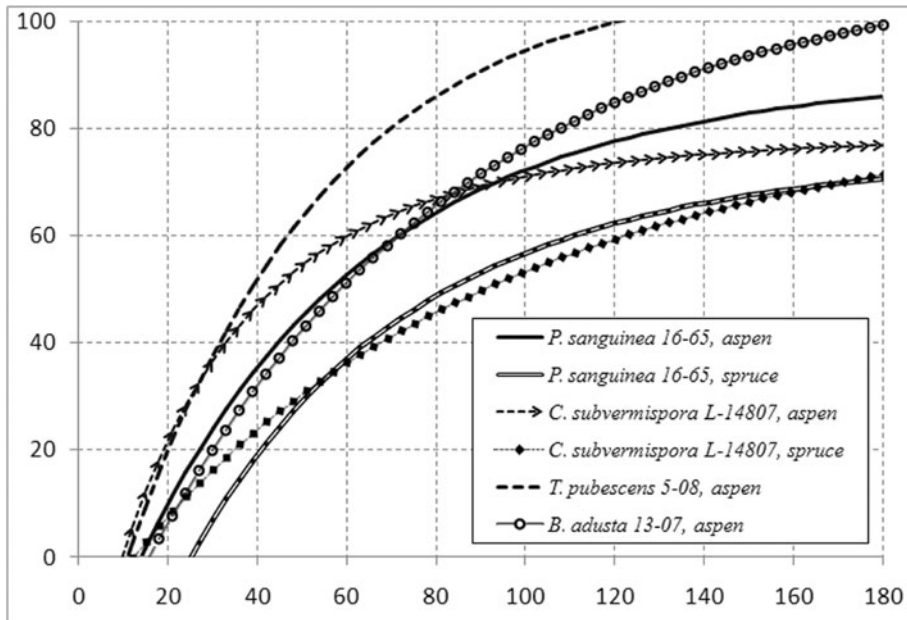


Fig. 2. Kinetic of lignin degradation during simultaneous and successive white rot: abscissa – time, days; ordinate – lignin weight loss, %.

cific rate of decomposition. The specific rates of decomposition of the aspen and spruce samples caused by *C. subvermispora* L-14807 SS-3 (aspen $k_2 = 6,2 \times 10^{-3} \text{ day}^{-1}$; spruce $k_2 = 4,1 \times 10^{-3} \text{ day}^{-1}$) were remarkably higher than the rates caused by *P. sanguinea* 16-65 (aspen $k_2 = 1,4 \times 10^{-3} \text{ day}^{-1}$; spruce $k_2 = 2,0 \times 10^{-3} \text{ day}^{-1}$). The specific rates of decomposition caused by successive white-rot fungi were found to be much lower when compared to those of simultaneous white-rot fungi *T. pubescens* 5-08 (aspen $k_2 = 22,3 \times 10^{-3} \text{ day}^{-1}$) and *B. adusta* 13-07 (aspen $k_2 = 14,2 \times 10^{-3} \text{ day}^{-1}$). The slow rate of wood decay caused by successive white-rot fungi was apparently predetermined by the selective character of lignin degradation. The slow wood decay observed during delignification corresponded to the period of exponential lignin degradation, which demands time and energy consumption. Lignin degradation during simultaneous white rot occurred with a linear dependency upon wood-mass loss and indicates a synchronous degradation of different wood constituents, which is common for this type of decay.

It is important to note that the specific rates of decomposition can be compared only when they are obtained using the same model. Parameters k_1 , k_2 , t_0 , and δ_{\max} are very sensitive to the experimental conditions and might vary within a wide range, depending upon the fungal strain, the temperature, amount of moisture, and other factors.

Models 6 and 7 provide a satisfying description of lignin degradation caused by lignin-degrading fungi. With the help of these models, we determined that simultaneous white-rot fungi degrade lignin in a linear relation-

ship to wood-mass loss, while the lignin degradation caused by successive white-rot fungi corresponds to an exponential dependency. The main drawback of the linear model is the impossibility to set the maximum lignin mass loss (δ_{Lmax}). It seems awkward to use two different models to describe lignin degradation caused by successive and simultaneous white-rot fungi, but it is difficult to find one model that describes, with one mathematical expression, processes that are so different.

Both groups of examined white-rot fungi are prospects for biotechnological applications. The nonspecific nature and high oxidative potential of simultaneous white-rot fungi enzymes seem to be irreplaceable for bioremediation processes that require fast recycling of organic wastes and pollutants. Also, for the purposes of the pulp and paper industry, which requires the selective removal of lignin from wood chips, natural features of the successive white-rot fungi can be useful.

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