

Article

Litter Decomposition and Nutrient Dynamics in Fire-Affected Larch Forests in the Russian Far East

Semyon Bryanin ^{*}, Anjelica Kondratova and Evgeniya Abramova

Institute of Geology and Nature Management, Far East Branch, Russian Academy of Sciences, Blagoveshchensk 675000, Russia; kondratova.ava@gmail.com (A.K.); lab.geoecology@mail.ru (E.A.)

* Correspondence: bruanin@gmail.com; Tel./Fax: +7-4162-225-325

Received: 2 July 2020; Accepted: 11 August 2020; Published: 13 August 2020



Abstract: Russian boreal forests hold a considerable carbon (C) stock and are subjected to frequent surface fires that unbalance C storage and ecosystem function. Although postfire ecological changes aboveground are well understood, biological C flows (e.g., decomposition in the postfire period) remain unclear. We present the results of a long-term field litterbag experiment on needle litter decomposition in typical *Larix gmelinii* boreal forests in the Russian Far East. For 3 years, we measured mass loss, C and nitrogen (N) concentrations, lignin and manganese dynamics, respiration intensity and enzyme activity in decaying needles, and environmental conditions (temperature and litter moisture). The decomposition rate at 850 days was 0.435 and 0.213 yr⁻¹ in a control forest and in a forest 15 years after a surface fire, respectively. Early stages of needle decay did not differ among sites, whereas decomposition slowed in later stages in burned forest relative to the control ($p < 0.01$). This was supported by hampered respiration, slow lignin accumulation in decaying needles, and low peroxidase activity in burned forest. We found no direct N release, and decaying litter immobilization was more pronounced in the control forest. In the later stages, we revealed restrained mass loss and associated C release from larch litter in burned forest. Slow and delayed N release may alter organic matter accumulation, the N cycle, and regeneration of the fire-disturbed larch ecosystem. Our investigations highlight hampered C flow from aboveground litter to soil humus even decades after surface fire in a larch ecosystem. Given the climate-induced increase of fire activity, C retained in the litter layer represents a pool that is more vulnerable to the next fire event.

Keywords: litter decomposition; Gmelin larch; boreal forest; forest fire; C; N

1. Introduction

Soils in boreal forests hold the most substantial pool of organic carbon (C) vulnerable to climate change. The consequences of modern unbalancing of this pool are likely to be substantial at the global scale. The estimates of soil C in the boreal zone vary from 700 to 1700 Pg, and boreal soil C is estimated to account for approximately 50% of the global soil organic matter [1–3]. This huge C storage is a part of the natural life-support system of the soil, and C is held in the soil in a balance of output and input processes. This equilibrium is vulnerable to modern climate change and is largely driven by human activity [4,5]. Among other influences, the increasing number of forest fires is considered to be the ambiguous factor affecting both stock and flows of C in boreal forests [6–8]. Therefore, we need to better understand the mechanism of C dynamics in fire-affected boreal ecosystems to predict the fate of the currently large C stock under the modern scenario of climate change.

Litter decomposition is the main energy and matter flow determining soil C accumulation and C dynamics in forests [9,10]. Decomposition is known to be a complex two-stage process of degradation and synthesis and is influenced by environmental and biological factors [11]. The first stage is controlled by environmental factors and is presumed to consist of mainly physical decay and leaching

of water-soluble substances, with a minor role being played by microorganisms. The later stage, which begins after mass loss reaches approximately 30%, is mainly related to the biodegradation of recalcitrant compounds. Of these, lignocellulose represents a major proportion of litter mass and is degraded by extracellular enzymes of certain microorganisms, mainly fungi [12,13]. It is known that fungal activity, including enzyme production, is mediated by soil environmental characteristics. For example, the abundance of fungi is increased in acidic media [14].

Another soil parameter that strongly regulates decomposition is the nitrogen (N) content, controlling both microbial activity and ecosystem primary productivity [15]. The initial N concentration in litter and its content in the organic layer are two important parameters predicting decomposition speed in boreal forests [16,17]. Contrary to the C dynamics, which are largely reflected in mass loss, the N dynamics have a distinct independent pattern [18]. The N dynamics during litter decomposition and N cycling are well understood in undisturbed forest ecosystems [19,20]. Immobilization and release patterns of N have important ecosystem consequences and vary substantially among ecosystems. Therefore, in nutrient-poor ecosystems, immobilization of N is the predominant process, especially in early stages of decomposition [21]. A comprehensive meta-analysis on the effect of fire on N pools in soil clearly shows that soil ammonium and nitrate levels are increased by fire, but the amount of total soil N is less affected [22]. A recent experiment on thermally altered pine needles has shown alterations in N dynamics during the decay process [23]. Given that fire leads to changes in the soil environment, the mechanism of decomposition and N dynamics, being well understood in natural conditions, could be considerably altered in fire-affected forests. Therefore, long-term effects of fire on immobilization and release of N during decomposition need to be evaluated in situ.

Fire alters soil properties and processes [24,25]; decomposition is not the exception, even though it is decoupled in time with fire events. Therefore, soil pH in the postfire period increases for up to a decade and is considered to suppress microbial activity and associated enzyme production [14,26]. Another study found that biodegradation function was suppressed in the fire-affected ecosystem at the decadal scale [27]. Direct investigation of litter decomposition in postfire forest ecosystems has received less attention. In burned boreal forests of Alaska and Scandinavia, several studies discovered restrained decomposition of black spruce and Scots pine litter [28–30]. Postfire litter decomposition in low-latitude coniferous forests is characterized by contradictory results. A litterbag study of pine litter decomposing in Arkansas, USA, revealed a minimal difference in mass loss and nutrient dynamics between burned and control forests [31]. Other research even found enhanced decomposition in a postfire period in the one-seed juniper woodland of New Mexico, USA [32]. All these works were conducted directly or a few years after forest fires, whereas the long-term legacy of fire remains largely unclear. Surface fires substantially thin vegetation cover and consequently increase insolation of the soil surface. This later directly affects the temperature and moisture of the litter layer, which are the most important determinants of decomposition. Another long-lasting legacy of fire is its byproducts such as charcoal and soot [33], recognized as important mediators of soil properties affecting the decomposition process [34,35]. Previous work has argued the importance of long-term investigation of nutrient cycling in the fire-return interval [27]. However, despite broad understanding, such investigations remain scarce, especially in the larch ecosystem, which holds one of the biggest C stocks in the boreal zone [36].

Larch (*Larix* spp.) forest, as the discontinuous continental ecosystem, covers approximately 2.9 million km² and represents a major proportion of the boreal forested area [37]. The huge soil C stock in these forests is a result of slow decomposition at low temperatures [38]. The larch ecosystem regularly experiences surface fires; however, larch trees usually survive and continue their functioning, producing needle-leaf litter [39]. Even though the larch ecosystem is adapted to fire, alteration of C dynamics in the fire-respite period remains the knowledge gap in understanding the C dynamics of the boreal larch forests. Therefore, litter decomposition in the postfire larch forests remains unknown, both directly after a fire event and in the long term. Decay processes in unburned larch stands have been investigated in plantations of Northwest China [40] and in Siberian permafrost larch stands. Most studies in postfire larch stands are related to alteration of the soil's physical and chemical properties

and microbiological activity of the litter layer [41–43]. These studies undoubtedly provide a certain background for understanding postfire forest dynamics affecting decomposition, but it is necessary to have direct field evidence of the decomposition mechanism and nutrient dynamics in postfire larch forests.

To obtain direct evidence of changes in the decomposition and nutrient dynamics in a larch forest after a fire, we performed a 3-year field experiment based on three hypotheses. Specifically, we hypothesized that (1) mass loss and related C release will not differ between burned and background forests during early decomposition stages; (2) the decomposition process in the burned forest will be decelerated in the late stages, resulting in suppressed C release from litter; and (3) N immobilization will dominate over the release of N, and this phenomenon will be more pronounced at the burned site, especially in the late decomposition stages. We tested these hypotheses with a 3-year field litterbag experiment in burned (15 years prior) and natural larch (*Larix gmelinii* Rupr.) forests in the Russian Far East.

2. Materials and Methods

2.1. Site Characteristics

The field experiment was conducted in Zeysky State Nature Reserve, which spans the Tukuringra mountain range in the Russian Far East. Natural larch/birch (*Betula platyphylla*)/(*L. gmelinii* Rupr.) stands represent the typical vegetation cover of Eastern Siberia and the Far East. Our research area (53°50' N, 127°10' E) was located on a gentle south-facing mountain slope that included two neighboring stands: one was a background larch/birch forest with evenly distributed tree species, and the other larch stand was damaged by a surface fire 15 years prior. The surface fire was long-lasting and consumed the litter layer, even killing part of the trees. The two forest stands were 800 m apart from each other. There was a clear border of fire between stands; within the intact and burned stands, we established the “control” and “burned” research plots, respectively. The size of each research plot was 50 × 50 m. Forest and soil characteristics of research plots differed even 15 years after the fire (Table 1). Thus, the stem number in the burned plot was more than 3 times lower than that of the control plot, and soil on burned plot had lower acidity and levels of dissolved nutrients. Average counts of functional groups of microorganisms in the burned plot were much lower than those of the control.

Table 1. Stand, soil, and litter characteristics.

Characteristic		Control	Burned
<i>Larix gmelinii</i> (Rupr.)			
Stem number ha ⁻¹		436	124
Basal area m ² ha ⁻¹		23.1	7.9
Mean D _{1.3} , cm		26	28
Mean height, m		19	19
<i>Betula platyphylla</i> Sukacz.			
Stem number ha ⁻¹		484	64
Basal area m ² ha ⁻¹		21.9	1.1
Mean D _{1.3} , cm		24	26
Mean height, m		21	18
<i>Soil Characteristics 0–10 cm</i>			
Total litter stock:	g m ⁻²	251 ± 20.4	94.4 ± 11.2
Water pH		4.8 ± 0.1	5.4 ± 0.1
Total organic C, %		20.1 ± 2.0	21.1 ± 2.9
Total N, %		0.77 ± 0.08	0.86 ± 0.11
Dissolved organic C, mg L ⁻¹		43.9 ± 4.35	24.1 ± 2.04
Dissolved organic N, mg L ⁻¹		1.11 ± 0.17	0.77 ± 0.09
<i>Average counts of microorganisms, CFU 10⁶g⁻¹dry litter</i>			
Micromycetes		2.1	0.8
Ammonifying bacteria		4.2	1.2
Oligotrophic bacteria		6.4	2.0
Actinomycetes		0.2	1.4

Study sites were distributed in the discontinuous permafrost soil region with a mean annual temperature of -0.7 °C. The minimum monthly average temperature occurs in January (-19.3 °C), with the maximum in July (19.1 °C). The sum of annual precipitation is 528 mm, the majority of which falls as rain from July to September [44]. The soil in the study area is classified as a Dystric Cambisol formed on granite rocks [45]. Soil in the intact condition is characterized by a thick (~ 10 cm) litter layer [46].

2.2. Litterbag Experiment

We used the litterbag approach to investigate the decomposition process of larch needles. Litterbags were made of white nylon with a mesh size of 50 μm . The bag size was 100 × 100 mm with sealed edges. We chose the 50- μm mesh size to prevent decomposed litter fragments and root ingrowth from washing out. This approach allowed us to focus on microbial and fungi decomposition. We selected litter material from larch tree species based on their domination of boreal forests of Eastern Eurasia. We used freshly fallen litter material collected in a forest adjacent to our research site for the experiment in both plots. We used identical litter types in both forests to focus on the fire-affected ecosystem function and avoid different litter chemistry, which strongly affects the decay process. Each bag contained approximately 7 g of air-dried litter in six replications per sampling date. The experiment began in May of 2016, and sampling was performed 75, 140, 500, and 850 days after the experiment began. The experiment ended in the fall of 2018.

During the entire decomposition period, we measured soil parameters such as temperature and water content. Soil temperature was measured hourly at a depth of 5 cm in three points on each site with a Tidbit v2 Temp Logger (Onset Computer Corporation, MA, USA). We measured gravimetric moisture by sampling soil beneath the litterbags on each sampling date. All laboratory procedures were conducted at the Analytical Center of Mineral-Geochemistry Investigation of the Institute of Geology and Nature Management, Far Eastern Branch of the Russian Academy of Sciences, Russia.

2.3. Mass Loss

We estimated mass loss as the difference between initial oven-dried mass and mass on each sampling day. In this study, decomposition rate was described by the decomposition constant (k), which was calculated using a single-exponential model [47]. A linear regression of the ratio of the ln-transformed remaining mass versus time allowed us to calculate the k value. As decomposition rate changes during decay process, we calculated the k value for the early stage of decomposition (0–140 days) and at the end of the experiment (850 days) to represent the whole decomposition period.

2.4. Litter Respiration

We used litter respiration as a proxy for microbiological activity [48]. The bags used in the experiment shielded the contained litter from penetration of roots and soil invertebrates, which allowed us to consider the carbon dioxide (CO₂) emissions from decomposing needles as the respiration of microorganisms mineralizing larch needles. Measurements of litter respiration were conducted over litterbags gathered at the end of the experiment on the 850th day. The CO₂ flux was measured under laboratory conditions at constant temperature of 22 °C with a closed static chamber system. The system comprised an infrared gas analyzer (IRGA, GMP343, Vaisala, Finland) attached to a 0.497-L cylindrical chamber. We enclosed one litterbag in the chamber and measured the CO₂ concentration for 5 min. To reduce the effects of air disturbance caused by opening the chamber, the data for the first and last 30 s were not used. We calculated the CO₂ flux (R , nmol CO₂ g⁻¹ s⁻¹) according to the method of Pumpanen et al. (2010) [49].

2.5. Chemical Analysis

The C and N concentrations in larch litter were analyzed using the combustion method with a TOC-L analyzer on a module for solid sample measurement (SSM-5000A, Shimadzu, Japan). Initial litter element concentrations were as follows: N, 0.38%; C, 44.5%; and C:N ratio, 117. To measure the lignin content, we employed Fourier transform infrared spectrometry (FTIR) with Fourier transform IR spectrometer Nicolet iS10 (Thermo Fisher, Waltham, MA, USA). Spectra were taken in the medium IR range (400–3700 cm⁻¹) with resolution of 4 cm⁻¹ and comprised an average of 100 scans. We compared FTIR absorption spectra of initial needle tree litter and the needles transformed during the decay process (frequency range was 1400–1800 cm⁻¹) to estimate lignin dynamics. This estimation was performed at the absorption band of ~1510 cm⁻¹. The 1510 cm⁻¹ band refers to skeleton vibrations of aromatic rings that represent the foundation of the C skeleton in the lignin structure [50,51]. Enzyme activity, namely peroxidase, is highly dependent on manganese (Mn) concentration in the litter. We therefore determined the Mn concentration in air-acetylene flame by atomic absorption (180-50S, Hitachi, Tokyo, Japan).

Peroxidase activity was measured as the rate of substrate oxidation in the presence of added hydrogen peroxide [52]. The measurement of peroxidase activity in soil was performed spectrophotometrically using pyrogallol (1, 2, 3-trihydroxybenzene) as the substrate, in accordance with previous research. The amount of purpurogallin formed was determined by taking the absorbance at 430 nm (LEKI SS 2107 spectrophotometer, MEDIORA OY, Finland). Total N and C concentrations in the soil and the needles were analyzed using the combustion method with a TOC-L analyzer with solid sample measurement module (SSM-5000A, Shimadzu).

2.6. Statistical Analysis

First, all data were checked for normality and homogeneity of variances. Differences in soil temperature were then tested by the Friedman rank-sum test. Differences in mass loss between sampling days were checked after data normalization by ANOVA following the Tukey HSD test. Correlation between element concentration and mass loss were estimated by the Pearson correlation

test after data normalization. All statistical analysis was performed in R-studio 1.1.383 R Core Team, Vienna, Austria [53].

3. Results

3.1. Mass Loss and Decomposition Constant

In the early stage of the experiment, larch needles decomposed at similar rates at both the control site and the burned site ($p = 0.507$), which resulted in a 25% loss of initial mass over the 140 days (Figure 1). In the later stages of decomposition, starting from the 500th day, a significant decrease of decomposition rate occurred in the burned forest ($p = 0.0021$), whereas no decrease occurred in the control. At the end of the experiment (850 days), mass loss at the control site (67.5%) was significantly greater than at the burned site (44.2%, $p = 0.0035$; Figure 1).

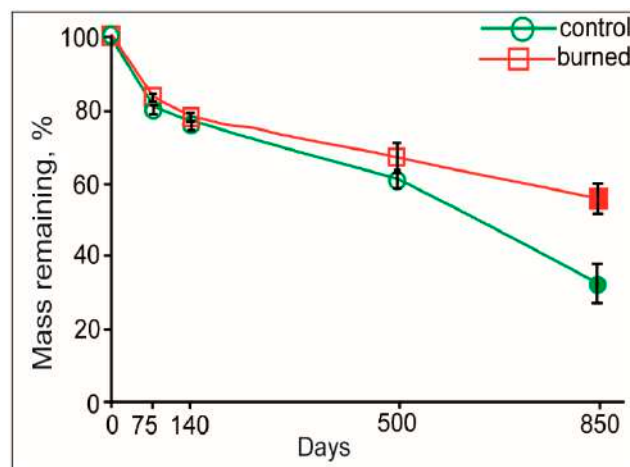


Figure 1. Mass loss of larch needles in burned and control stands. Error bars represent \pm SE ($n = 6$). Filled markers denote significant differences ($p < 0.05$ based on ANOVA followed by Tukey HSD).

The decomposition constant at the burned site was slightly lower in the early period and two times lower at the end of the experiment compared with the control site (Table 2).

Table 2. Mass remaining and decomposition constant (k , year^{-1}) for two study sites. Data are means \pm SE ($n = 6$).

Period (days)	Control			Burned		
	Mass Loss (%)	k (year^{-1})	r^2	Mass Loss (%)	k (year^{-1})	r^2
140	23.4 ± 2.02	0.714	0.92	21.9 ± 1.49	0.658	0.96
850	67.5 ± 5.18	0.435	0.96	44.2 ± 3.83	0.219	0.92

3.2. Soil Temperature and Moisture

At the burned site, soil temperature at 5 cm depth was 3–7 °C lower than the control during the winter season ($p < 0.001$; Figure 2). Summer temperatures did not differ for the first 2 years, but the average summer temperature in the late decomposition period (i.e., the third year of the experiment) was 2 °C higher at the burned site than at the control site ($p < 0.001$). The water content in litter bags at the burned site was lower over the entire period of the experiment ($p < 0.001$; Figure 3a). At the burned site, the water content and mass loss values showed stronger correlation ($R^2 = 0.42$, $p < 0.001$) when compared with those of the control site ($R^2 = 0.29$, $p < 0.05$; Figure 3b).

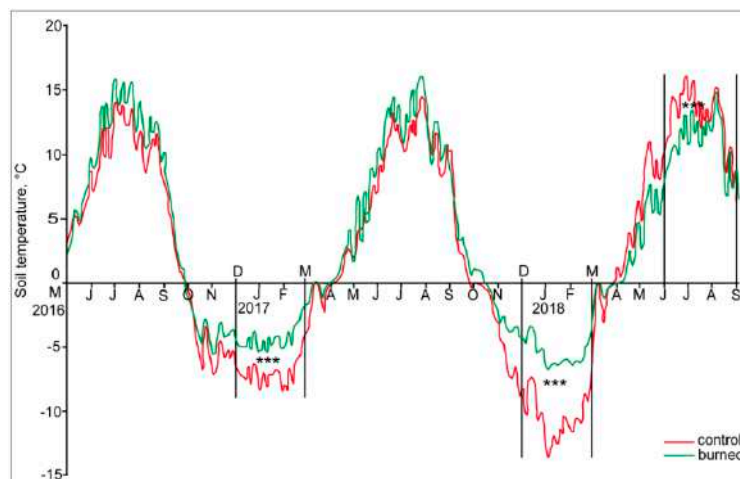


Figure 2. Daily average soil temperature at 5 cm depth during the 3-year decomposition experiment. Uppercase letters on the axis denote months of the year. Asterisks represent significant differences of soil temperatures in given periods based on the Friedman rank-sum test.

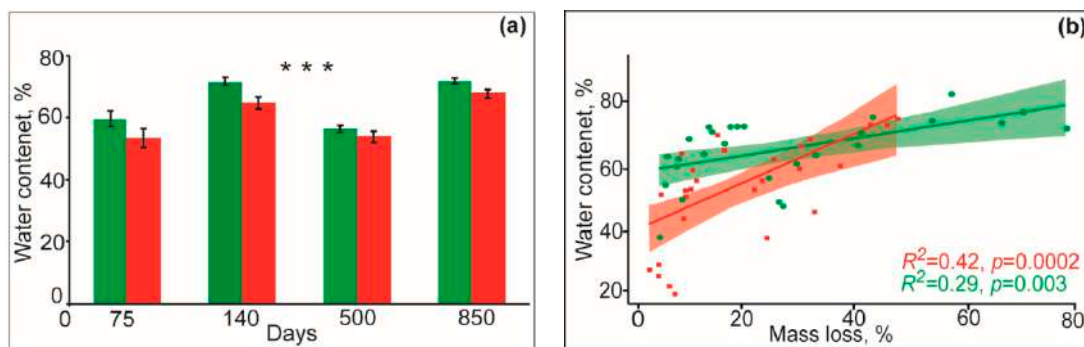


Figure 3. Litterbag water content (a) during decomposition experiment. Error bars represent \pm SE ($n = 6$). Asterisks indicate significant differences (Holm–Bonferroni corrected $p < 0.05$) during the entire decomposition period, based on a generalized linear mixed model (GLMM) where ‘days’ was set as a random factor. (b) Linear relationship between water content and mass loss of the needles during entire decomposition period. Red and green areas represent the 95% confidence intervals in the burned and control stands, respectively.

3.3. Dynamics of C, N, and C:N Ratio

Initially, the same pattern of N dynamics was seen in both sites, but the N concentration during the entire experiment was higher in litter bags from the control site than in those from the burned site. The N concentration showed a distinct increment by the 500th day of the experiment, where we recorded 1.5 times lower N concentration at the burned site (1.1%) than at the control site (1.6%) ($p = 0.0417$; Figure 4a). The N concentration decreased in the later stage of decomposition. At the end of the experiment, the difference in N concentration between the sites remained significant ($p = 0.0234$). The correlation between the N concentration and mass loss showed a similar pattern for both sites (Figure 4b).

The magnitude and pattern of C release during decomposition were site-dependent. Litter at the control site had eventually lost a larger proportion of initial C than litter at the burned site ($p < 0.001$; Figure 4c). The pattern of C release at the burned site differed from that of the control site; C release at the burned site was much faster initially ($p < 0.001$ on the 75 days) but then was reduced in the last 2 years. After 3 years of decomposition, litter at the burned site had lost just 36% of its initial C.

Carbon related to mass loss also showed a distinct site-dependent pattern. At the control site, C tended to be released during decomposition, whereas we observed pronounced accumulation at the burned site at the end of the experiment (Figure 4d).

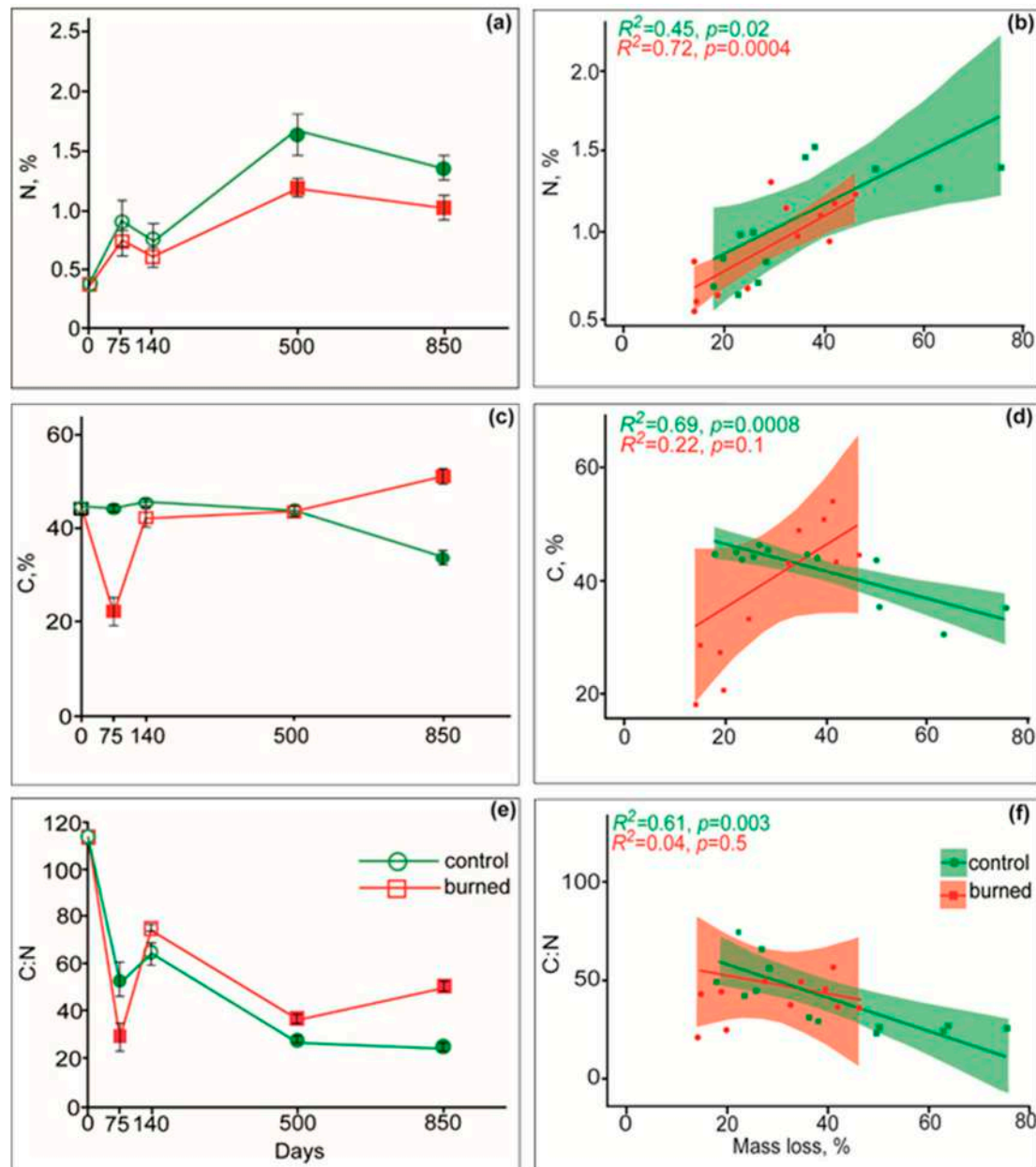


Figure 4. Dynamics of nutrient concentrations (a,c,e) and linear relationship between the mass loss and concentrations of C (b) and N (d) and the C:N ratio (f) in the control and burned stands. Error bars represent \pm SE ($n = 6$). Filled markers denote significant differences ($p < 0.05$ based on ANOVA followed by Tukey HSD). Red and green areas represent the 95% confidence intervals in the burned and control stands, respectively.

The C:N ratio declined exponentially, and it was especially distinct at the beginning of the experiment, having declined 2-fold during the first 75 days. However, the C:N ratio for the burned site at the end of the experiment (850 days) was twice as high (45) as that of the control site (20; Figure 4e). The increase of mass loss showed a distinct decreasing C:N ratio at the control site, whereas the burned site showed a very slight and nonsignificant decreasing trend (Figure 4f).

3.4. Lignin and Mn Dynamics

The lignin concentration increased compared with initial values to almost the same values for both sites at the end of the experiment. At the control site, the lignin concentration increased evenly during the whole experiment. However, its trend was multidirectional at the burned site, and the relative concentrations were lower on the 500th and 850th days when compared with the control (Figure 5).

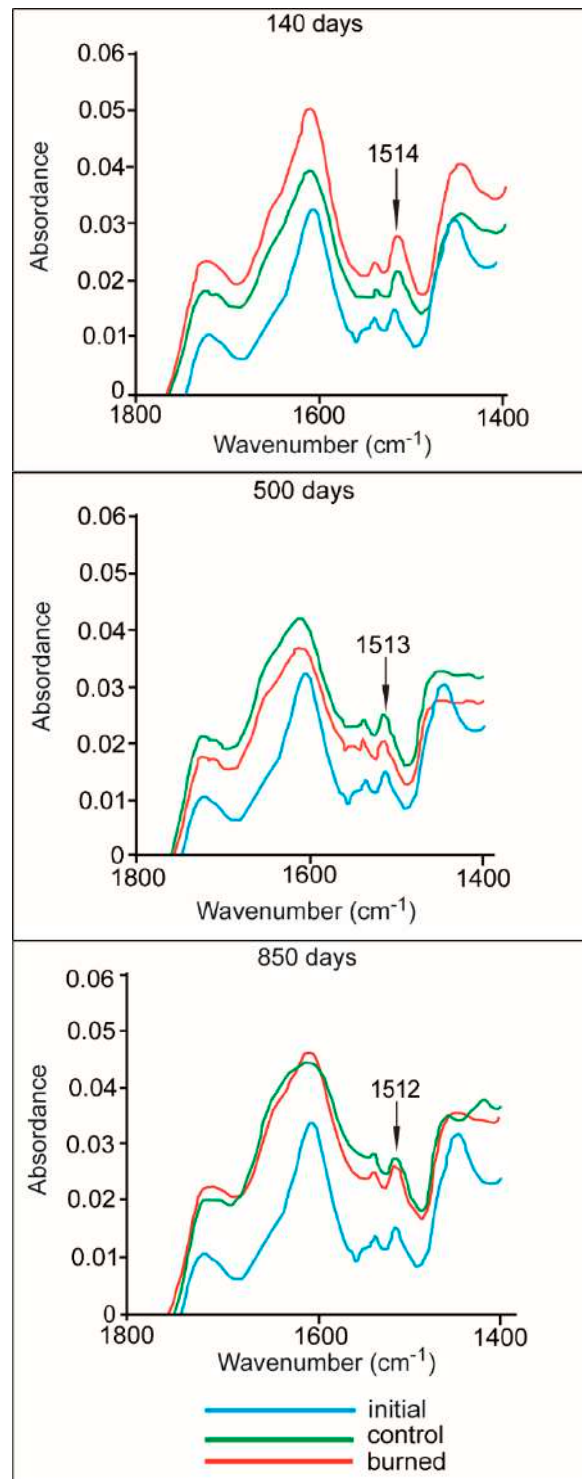


Figure 5. Fourier transformed infrared spectrum of needle litter at different stages of decomposition. Each line represents the arithmetic mean of spectra ($n = 3$).

The Mn concentration decreased during decomposition at both the control and burned sites. In the early stage of decomposition, the Mn concentration did not differ substantially between the sites ($p = 0.21$; Figure 6b). From the 500th day of the experiment until the end of the experiment, the Mn concentration at the burned site decreased faster than at the control site.

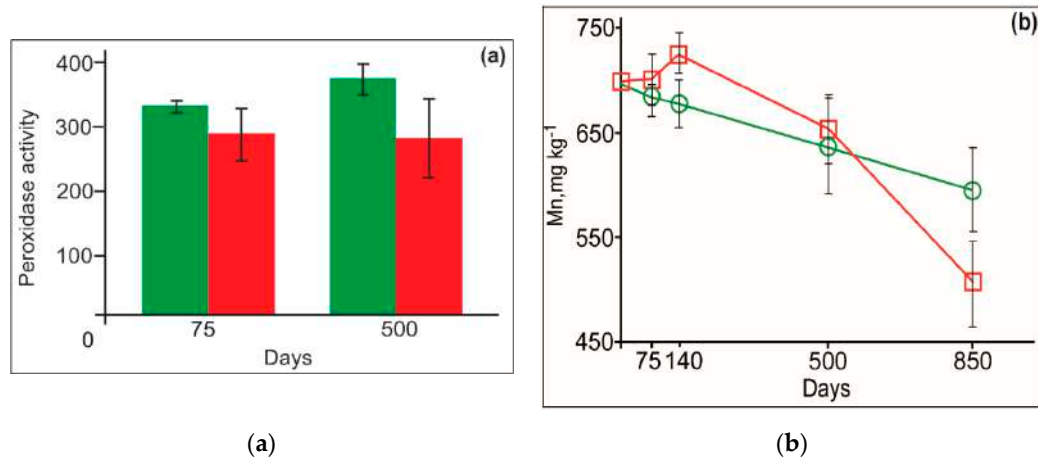


Figure 6. Peroxidase activity (a) (mg of purpurogallin per 100 g of soil in 30 min) in litterbags on the sampling dates. Data in the figure denote the mean sample combined from six individual litterbags. Dynamics of Mn concentration (b) during the decomposition experiment. Error bars represent \pm SE ($n = 6$).

3.5. Litter Respiration and Enzyme Activities

At the control site, total peroxidase activity on the 500th day of decomposition was 1.3 times that of the burned site (Figure 6a). Litter respiration in the later stage of decomposition (850 days) varied depending on site. At the burned site, CO₂ emissions were 1.5-fold lower than those of the control site ($p = 0.0207$; Figure 7).

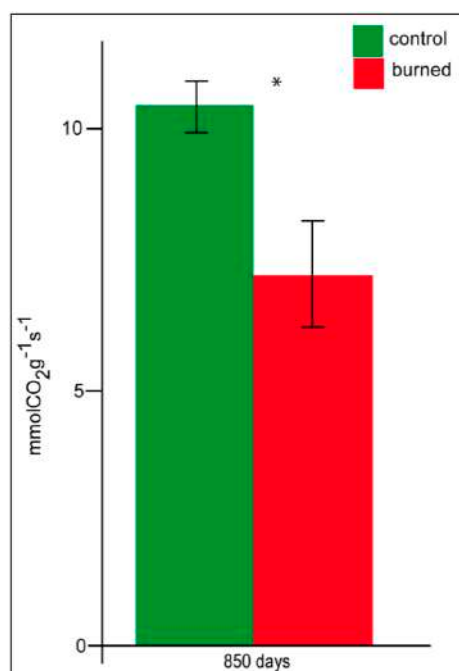


Figure 7. Respiration of litter on the 850th day of the decomposition experiment. The asterisk indicates a significant difference according Tukey's HSD test following ANOVA ($p \leq 0.05$). Error bars represent \pm SE ($n = 6$).

4. Discussion

We found much slower litter decomposition in the surface-burned (15 years since the fire) forest, compared with the undisturbed stand, resulting from moderation of the process in the late stage of decomposition. At the end of the experiment (nearly 3 years), the decomposition constant (k) in the undisturbed forest was two times higher (0.435 yr^{-1}) than that in the burned forest. The decomposition rate in the control forest was close to that given in the generalized data of Zhang et al. (2018) [54] for coniferous forests ($\sim 0.400 \text{ yr}^{-1}$). However, in the burned forest, our calculated rate was similar to that of larch stands in Siberia (0.180 yr^{-1}), which are considered to have a low biodegradation rate [55]. Therefore, our results suggest that fire can reduce decomposition rates in larch forest, even 15 years after the fire.

Although we observed slower decomposition in the burned forest, this did not extend over the whole experimental period, where two different stages were observed. Initially, litter decomposed at the same rate in both stands, having lost 25% of the initial mass by 140 days. This rapid mass loss at the beginning has been commonly reported in decay studies in boreal forests. In a decomposition study in Fennoscandia, decomposing pine needles rapidly lost highly soluble compounds due to leaching and microbiological growth in the first stage of decomposition until 25–30% of mass had been lost [11]. At this stage, climatic conditions and concentration of the main nutrients, especially N, greatly influenced the decomposition rate. In our study, the lack of differences in mass loss at the beginning suggests that litter quality (as we used identical litter) and/or environmental factors, but not fire-altered ecosystem function, influenced the early decomposition stage. We first detected differences in mass loss and nutrient dynamics in the second year of the experiment, highlighting the value of long-term field experiments to reveal the postfire effect in the later decomposition stages. The decomposition rate was reduced in the late stages after easily degradable compounds were consumed in the early period [11]. In these later stages, the remaining substrate was largely made up of recalcitrant compounds, such as lignocellulose, which can be degraded by limited types of microorganisms that produce specific extracellular enzymes [56]. Among these, peroxidases are essential lignin-decomposing enzymes [57]. The lower peroxidase activity observed during the whole experiment at the burned site could explain the restrained decomposition of lignin and associated substances (Figure 5). At the same time, low peroxidase activity in the burned forest suggests that the surface fire likely modified soil parameters that, in turn, regulate enzyme production.

Decomposer activity and functioning have been shown to be altered in response to fire-caused changes of soil environment, which can last up to decades [27,30,58]. For example, increases in soil pH in the postfire period have been thought to suppress microbial activity and associated enzyme production [14,26]. Moreover, high-pH media decreases mobility of Mn, which is the essential element for enzyme production [59] and is known as a mediator of catalytic activity of ligninolytic enzymes: manganese peroxidase, lignin peroxidase, and laccase [12,13,60]. Berg (2014) demonstrated a positive correlation between mass loss and Mn concentration increase in pine needles in the late stages of decomposition. In our experiment, we observed lower microbial activity in litterbags at the burned site (Figure 7), and the number of microbial trophic groups was decreased by up to 3.5 times (Table 1). We observed significantly higher litter pH in the postfire stand compared with the control (pH 5.3 and 4.8 respectively, $p < 0.001$; Table 1). This difference could explain the lower Mn mobility and related lower peroxidase activity observed in the litter bags in burned forest (Figure 6) and thus the low rate of decomposition of recalcitrant compounds.

Decomposition of organic matter, as an important ecosystem function, is related to nutrient dynamics, particularly of N, influencing the microbial and plant communities. Therefore, understanding the changes in the N concentration can help to determine how fast it is being immobilized or released from decaying substrate. Investigations in US loblolly pine forests showed slow N release: 27–34% of the initial amount was released over 8 years [61]. In our experiment, there was no direct N release in either of the sites over the 3-year period (Figure 4a). On the 500th day of the experiment, we observed more immobilization at the control site (263% of the initial N mass) compared to the burned site (209%).

Similar to our findings, a litterbag study in a pine forest of Central Poland found that pronounced N immobilization occurred in undisturbed stands compared with disturbed ones [62]. By the end of our experiment, the N amount in litterbags was 115% of the initial N mass at the control site and 149% of the initial N mass at the burned site. Again, the reason for this discrepancy could be the inhibition of microbial groups responsible for degradation of recalcitrant compounds. More N accumulation in larch needles at the control site compared with the burned site may have occurred because of N translocation by fungi and increased fixation by bacteria in the favorable intact environment [10,63,64]. The amount of available N in the litter layer could significantly influence its immobilization into freshly fallen N-poor litter [65,66]. According to our data, the concentration of water-soluble N in the litter layer of the control site was 1.4 times higher than that of the burned site (Table 1). Low N availability in the litter layer could explain the stronger correlation between N and mass loss at the burned site, suggesting that N is a limiting factor in decomposition in postfire forest (Figure 4b). Thus, our data showed that in the undisturbed larch stand N was released more quickly from decaying litter. This release causes an increased N availability for the plants and microorganisms. In contrast, the rate of N release slowed down in the burned stand, which would result in reduced availability for plants.

In summary, our results show no changes in early-stage decomposition between stand types but clearly restrained late-stage decomposition of larch litter in the burned stand. Such long-lasting fire consequences (i.e., 15 years) influence both C release and N cycling in the boreal forest. Immobilization processes dominated over release in both stands, but immobilization was more pronounced at the burned site, suggesting a more restrained N cycle. This restriction could eventually influence plant nutrition and microbial activity. The restrained respiration and C release at the burned site suggests longer C retention in the litter layer. This could have several consequences for the ecosystem, either positive or negative. Restrained respiration denotes slower decomposition, which positively affects forest function as a C sink. Under these conditions, C slowly undergoes humus formation and consequently does not turn to the stable organic matter pool for some time. However, the retention of C in the litter pool is not an optimal C storage strategy from the viewpoint of current climate change, as recurrent forest fires, whose frequency has been predicted to increase, result in increased C emissions to the atmosphere in the form of CO₂. Together, our results provide insights into the current understanding of mechanisms of the C cycle in the little-studied fire-affected larch forests. In terms of future research, gaining a better understanding of the proportion of litter C that is transformed into soil humus in these forests is worth pursuing.

Author Contributions: S.B. and E.A. conceived and designed the study. S.B. and A.K. wrote and revised the manuscript. All authors have read and agreed to the published version of the manuscript.

Funding: The reported study was funded by Russian Foundation for Basic Research according to the research project 19-05-00305 to Bryanin S.V. and 18-35-00454 to Abramova E.R.

Acknowledgments: Authors thank the staff of Zeysky State Nature Reserve, especially Lisovskii V.V., for invaluable support during stand selection and experiment establishment. We express our gratitude to Rozhdestvina V.I., Piletskaya O.A., and Borodina N.A. for their assistance in analytical assays; Smuskina I.N. for data analysis; and Martynov A.V. for FTIR spectra analysis. We thank Alex Boon from Edanz Group (www.edanzediting.com/ac) for editing a draft of this manuscript.

Conflicts of Interest: The authors declare no conflict of interest.

References

1. Pimm, S.; Roulet, N.; Weaver, A. Boreal forests' carbon stores need better management. *Nature* **2009**, *462*, 276. [[CrossRef](#)] [[PubMed](#)]
2. Tarnocai, C.; Canadell, J.G.; Schuur, E.A.G.; Kuhry, P.; Mazhitova, G.; Zimov, S. Soil organic carbon pools in the northern circumpolar permafrost region. *Global Biogeochem. Cycles* **2009**, *23*. [[CrossRef](#)]
3. DeLuca, T.H.; Boisvenue, C. Boreal forest soil carbon: Distribution, function and modelling. *Forestry* **2012**, *85*, 161–184. [[CrossRef](#)]

4. Davidson, E.A.; Janssens, I.A. Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. *Nature* **2006**, *440*, 165–173. [[CrossRef](#)]
5. Lawrence, D.M.; Slater, A.G.; Romanovsky, V.E.; Nicolsky, D.J. Sensitivity of a model projection of near-surface permafrost degradation to soil column depth and representation of soil organic matter. *J. Geophys. Res.* **2008**, *113*, F02011. [[CrossRef](#)]
6. Kasischke, E.S.; Christensen, N.L.; Stocks, B.J. Fire, Global Warming, and the Carbon Balance of Boreal Forests. *Ecol. Appl.* **1995**, *5*, 437–451. [[CrossRef](#)]
7. Schaphoff, S.; Reyer, C.P.O.; Schepaschenko, D.; Gerten, D.; Shvidenko, A. Tamm Review: Observed and projected climate change impacts on Russia's forests and its carbon balance. *For. Ecol. Manag.* **2015**, *361*, 432–444. [[CrossRef](#)]
8. Dove, N.C.; Safford, H.D.; Bohlman, G.N.; Estes, B.L.; Hart, S.C. High-severity wildfire leads to multi-decadal impacts on soil biogeochemistry in mixed-conifer forests. *Ecol. Appl.* **2020**. [[CrossRef](#)]
9. Wardle, D.A.; Nilsson, M.-C.; Zackrisson, O.; Gallet, C. Determinants of litter mixing effects in a Swedish boreal forest. *Soil Biol. Biochem.* **2003**, *35*, 827–835. [[CrossRef](#)]
10. Bani, A.; Pioli, S.; Ventura, M.; Panzacchi, P.; Borruso, L.; Tognetti, R.; Tonon, G.; Brusetti, L. The role of microbial community in the decomposition of leaf litter and deadwood. *Appl. Soil Ecol.* **2018**, *126*, 75–84. [[CrossRef](#)]
11. Berg, B.; McClaugherty, C. *Plant Litter: Decomposition, Humus Formation, Carbon Sequestration*, 3rd ed.; Springer: Berlin/Heidelberg, Germany, 2014; ISBN 978-3-642-38820-0.
12. Perez, J.; Jeffries, T.W. Roles of manganese and organic acid chelators in regulating lignin degradation and biosynthesis of peroxidases by *Phanerochaete chrysosporium*. *Appl. Environ. Microbiol.* **1992**, *58*, 2402–2409. [[CrossRef](#)] [[PubMed](#)]
13. Valášková, V.; Šnajdr, J.; Bittner, B.; Cajthaml, T.; Merhautová, V.; Hofrichter, M.; Baldrian, P. Production of lignocellulose-degrading enzymes and degradation of leaf litter by saprotrophic basidiomycetes isolated from a *Quercus petraea* forest. *Soil Biol. Biochem.* **2007**, *39*, 2651–2660. [[CrossRef](#)]
14. Hobbie, S.E.; Gough, L. Litter decomposition in moist acidic and non-acidic tundra with different glacial histories. *Oecologia* **2004**, *140*, 113–124. [[CrossRef](#)] [[PubMed](#)]
15. Averill, C.; Waring, B. Nitrogen limitation of decomposition and decay: How can it occur? *Glob. Chang. Biol.* **2018**, *24*, 1417–1427. [[CrossRef](#)]
16. Melillo, J.M.; Aber, J.D.; Muratore, J.F. Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. *Ecology* **1982**, *63*, 621–626. [[CrossRef](#)]
17. Bradford, M.A.; Berg, B.; Maynard, D.S.; Wieder, W.R.; Wood, S.A. Understanding the dominant controls on litter decomposition. *J. Ecol.* **2016**, *104*, 229–238. [[CrossRef](#)]
18. Moore, T.R.; Trofymow, J.A.; Siltanen, M.; Prescott, C.; Group, C.W. Patterns of decomposition and carbon, nitrogen, and phosphorus dynamics of litter in upland forest and peatland sites in central Canada. *Can. J. For. Res.* **2005**, *35*, 133–142. [[CrossRef](#)]
19. Berg, B.; Söderström, B. Fungal biomass and nitrogen in decomposing scots pine needle litter. *Soil Biol. Biochem.* **1979**, *11*, 339–341. [[CrossRef](#)]
20. Schimel, J.P.; Bennett, J. NITROGEN MINERALIZATION: CHALLENGES OF A CHANGING PARADIGM. *Ecology* **2004**, *85*, 591–602. [[CrossRef](#)]
21. García-Palacios, P.; Shaw, E.A.; Wall, D.H.; Hättenschwiler, S. Contrasting mass-ratio vs. niche complementarity effects on litter C and N loss during decomposition along a regional climatic gradient. *J. Ecol.* **2017**, *105*, 968–978. [[CrossRef](#)]
22. Wan, S.; Hui, D.; Luo, Y. Fire Effects on Nitrogen Pools and Dynamics in Terrestrial Ecosystems: A Meta-Analysis. *Ecol. Appl.* **2001**, *11*, 1349. [[CrossRef](#)]
23. Stirling, E.; Smernik, R.J.; Macdonald, L.M.; Cavagnaro, T.R. Fire influences needle decomposition: Tipping point in *Pinus radiata* carbon chemistry and soil nitrogen transformations. *Soil Biol. Biochem.* **2019**, *135*, 361–368. [[CrossRef](#)]
24. Neary, D.G.; Klopatek, C.C.; DeBano, L.F.; Ffolliott, P.F. Fire effects on belowground sustainability: A review and synthesis. *For. Ecol. Manag.* **1999**, *122*, 51–71. [[CrossRef](#)]
25. Certini, G. Effects of fire on properties of forest soils: A review. *Oecologia* **2005**, *143*, 1–10. [[CrossRef](#)]

26. Switzer, J.M.; Hope, G.D.; Grayston, S.J.; Prescott, C.E. Changes in soil chemical and biological properties after thinning and prescribed fire for ecosystem restoration in a Rocky Mountain Douglas-fir forest. *For. Ecol. Manag.* **2012**, *275*, 1–13. [[CrossRef](#)]
27. Hart, S.C.; DeLuca, T.H.; Newman, G.S.; MacKenzie, M.D.; Boyle, S.I. Post-fire vegetative dynamics as drivers of microbial community structure and function in forest soils. *For. Ecol. Manag.* **2005**, *220*, 166–184. [[CrossRef](#)]
28. Berg, B. Litter decomposition and organic matter turnover in northern forest soils. *For. Ecol. Manag.* **2000**, *133*, 13–22. [[CrossRef](#)]
29. Holden, S.R.; Gutierrez, A.; Treseder, K.K. Changes in Soil Fungal Communities, Extracellular Enzyme Activities, and Litter Decomposition Across a Fire Chronosequence in Alaskan Boreal Forests. *Ecosystems* **2013**, *16*, 34–46. [[CrossRef](#)]
30. Köster, K.; Berninger, F.; Heinonsalo, J.; Lindén, A.; Köster, E.; Ilvesniemi, H.; Pumpanen, J. The long-term impact of low-intensity surface fires on litter decomposition and enzyme activities in boreal coniferous forests. *Int. J. Wildl. Fire* **2016**, *25*, 213. [[CrossRef](#)]
31. Liechty, H.O.; Reinke, M. The influence of repeated prescribed fire on decomposition and nutrient release in uneven-aged loblolly–shortleaf pine stands. *Fire Ecol.* **2020**, *16*, 6. [[CrossRef](#)]
32. Throop, H.L.; Abu Salem, M.; Whitford, W.G. Fire enhances litter decomposition and reduces vegetation cover influences on decomposition in a dry woodland. *Plant Ecol.* **2017**, *218*, 799–811. [[CrossRef](#)]
33. Preston, C.M.; Schmidt, M.W.I. Black (pyrogenic) carbon: A synthesis of current knowledge and uncertainties with special consideration of boreal regions. *Biogeosciences* **2006**, *3*, 397–420. [[CrossRef](#)]
34. Makoto, K.; Hirobe, M.; DeLuca, T.H.; Bryanin, S.V.; Procopchuk, V.F.; Koike, T. Effects of fire-derived charcoal on soil properties and seedling regeneration in a recently burned *Larix gmelinii*/Pinus sylvestris forest. *J. Soils Sediments* **2011**, *11*, 1317–1322. [[CrossRef](#)]
35. Bryanin, S.; Abramova, E.; Makoto, K. Fire-derived charcoal might promote fine root decomposition in boreal forests. *Soil Biol. Biochem.* **2018**, *116*, 1–3. [[CrossRef](#)]
36. Permafrost Ecosystems; Osawa, A.; Zyryanova, O.A.; Matsuura, Y.; Kajimoto, T.; Wein, R.W. (Eds.) *Ecological Studies*; Springer: Dordrecht, The Netherlands, 2010; Volume 209, ISBN 978-1-4020-9692-1.
37. Kobak, K.I.; Turchinovich, I.Y.; Kondrasheva, N.Y.; Schulze, E.D.; Schulze, W.; Koch, H.; Vygodskaya, N.N. Vulnerability and adaptation of the larch forest in Eastern Siberia to climate change. *Water. Air. Soil Pollut.* **1996**, *92*, 119–127. [[CrossRef](#)]
38. Kajimoto, T.; Matsuura, Y.; Sofronov, M.a.; Volokitina, a.V.; Mori, S.; Osawa, a.; Abaimov, a.P. Above- and belowground biomass and primary productivity of a *Larix gmelinii* stand near Tura, central Siberia. *Tree Physiol.* **1999**, *19*, 815–822. [[CrossRef](#)]
39. Goldammer, J.G.; Furyaev, V.V. *Fire in Ecosystems of Boreal Eurasia: Ecological Impacts and Links to the Global System*; Springer: Dordrecht, The Netherlands, 1996; pp. 1–20.
40. Zhang, W.; Yang, K.; Lyu, Z.; Zhu, J. Microbial groups and their functions control the decomposition of coniferous litter: A comparison with broadleaved tree litters. *Soil Biol. Biochem.* **2019**, *133*, 196–207. [[CrossRef](#)]
41. Ludwig, S.M.; Alexander, H.D.; Kielland, K.; Mann, P.J.; Natali, S.M.; Ruess, R.W. Fire severity effects on soil carbon and nutrients and microbial processes in a Siberian larch forest. *Glob. Chang. Biol.* **2018**, *24*, 5841–5852. [[CrossRef](#)]
42. Hu, T.; Hu, H.; Li, F.; Zhao, B.; Wu, S.; Zhu, G.; Sun, L. Long-term effects of post-fire restoration types on nitrogen mineralisation in a Dahurian larch (*Larix gmelinii*) forest in boreal China. *Sci. Total Environ.* **2019**, *679*, 237–247. [[CrossRef](#)]
43. Kong, J.; Yang, J.; Cai, W. Topography controls post-fire changes in soil properties in a Chinese boreal forest. *Sci. Total Environ.* **2019**, *651*, 2662–2670. [[CrossRef](#)]
44. Amur Center for Hydrometeorology and Environmental Monitoring. *Meteorological Characteristics of Zeya Meteorological Station between 1989 and 2011*; Amur Center for Hydrometeorology and Environmental Monitoring: Blagoveschensk, Russia, 2015.
45. WRB, I.W.G. *World Reference Base for Soil Resources 2014 International Soil Classification System for Naming Soils and Creating Legends for Soil Maps*; FAO: Rome, Italy, 2014; Volume 106, ISBN 978-92-5-108369-7.
46. Procopchuk, V.F.; Bryanin, S.V. Ecological Stability of Brown Raw-humus Taiga Soils in Relation to Anthropogenic Influences in Northern Part of Amur Region. *Eurasian J. For. Res.* **2007**, *10*, 85–88.

47. Olson, J.S. Energy Storage and the Balance of Producers and Decomposers in Ecological Systems. *Ecology* **1963**, *44*, 322–331. [[CrossRef](#)]
48. Gartner, T.B.; Cardon, Z.G. Decomposition dynamics in mixed-species leaf litter. *Oikos* **2004**, *104*, 230–246. [[CrossRef](#)]
49. Pumpanen, J.; Longdoz, B.L.; Kutsch, W. Field measurements of soil respiration: Principles and constraints, potentials and limitations of different methods. In *Soil Carbon Dynamics*; Kutsch, W.L., Bahn, M., Heinemeyer, A., Eds.; Cambridge University Press: Cambridge, UK, 2010; pp. 16–33. ISBN 9780511711794.
50. Pandey, K.K. A study of chemical structure of soft and hardwood and wood polymers by FTIR spectroscopy. *J. Appl. Polym. Sci.* **1999**, *71*, 1969–1975. [[CrossRef](#)]
51. Ouatmane, A.; Provenzano, M.R.; Hafidi, M.; Senesi, N. Compost Maturity Assessment Using Calorimetry, Spectroscopy and Chemical Analysis. *Compost Sci. Util.* **2000**, *8*, 124–134. [[CrossRef](#)]
52. Burns, R.G.; DeForest, J.L.; Marxsen, J.; Sinsabaugh, R.L.; Stromberger, M.E.; Wallenstein, M.D.; Weintraub, M.N.; Zoppini, A. Soil enzymes in a changing environment: Current knowledge and future directions. *Soil Biol. Biochem.* **2013**, *58*, 216–234. [[CrossRef](#)]
53. *R: A Language and Environment for Statistical Computing*; R Foundation for Statistical Computing: Vienna, Austria, 2017.
54. Zhang, W.; Gao, D.; Chen, Z.; Li, H.; Deng, J.; Qiao, W.; Han, X.; Yang, G.; Feng, Y.; Huang, J. Substrate quality and soil environmental conditions predict litter decomposition and drive soil nutrient dynamics following afforestation on the Loess Plateau of China. *Geoderma* **2018**, *325*, 152–161. [[CrossRef](#)]
55. Prokushkin, S.G.; Prokushkin, A.S.; Sorokin, N.D. The intensity of phytodetrite decomposition in larch forest of the permafrost zone in Central Siberia. *Biol. Bull.* **2014**, *41*, 89–97. [[CrossRef](#)]
56. Wang, W.; Zhang, Q.; Sun, X.; Chen, D.; Insam, H.; Koide, R.T.; Zhang, S. Effects of mixed-species litter on bacterial and fungal lignocellulose degradation functions during litter decomposition. *Soil Biol. Biochem.* **2020**, *141*, 107690. [[CrossRef](#)]
57. Johnsen, A.R.; Jacobsen, O.S. A quick and sensitive method for the quantification of peroxidase activity of organic surface soil from forests. *Soil Biol. Biochem.* **2008**, *40*, 814–821. [[CrossRef](#)]
58. Dove, N.C.; Hart, S.C. Fire Reduces Fungal Species Richness and In Situ Mycorrhizal Colonization: A Meta-Analysis. *Fire Ecol.* **2017**, *13*, 37–65. [[CrossRef](#)]
59. Heim, A.; Frey, B. Early stage litter decomposition rates for Swiss forests. *Biogeochemistry* **2004**, *70*, 299–313. [[CrossRef](#)]
60. Archibald, F.; Roy, B. Production of manganic chelates by laccase from the lignin-degrading fungus *Trametes (Coriolus) versicolor*. *Appl. Environ. Microbiol.* **1992**, *58*, 1496–1499. [[CrossRef](#)] [[PubMed](#)]
61. Jorgensen, J.R.; Wells, C.G.; Metz, L.J. Nutrient Changes in Decomposing Loblolly Pine Forest Floor. *Soil Sci. Soc. Am. J.* **1980**, *44*, 1307–1314. [[CrossRef](#)]
62. Horodecki, P.; Jagodziński, A.M. Site Type Effect on Litter Decomposition Rates: A Three-Year Comparison of Decomposition Process between Spoil Heap and Forest Sites. *Forests* **2019**, *10*, 353. [[CrossRef](#)]
63. Petrillo, M.; Cherubini, P.; Sartori, G.; Abiven, S.; Ascher, J.; Bertoldi, D.; Camin, F.; Barbero, A.; Larcher, R.; Egli, M. Decomposition of norway spruce and european larch coarse woody debris (CWD) in relation to different elevation and exposure in an alpine setting. *IForest* **2016**, *9*, 154–164. [[CrossRef](#)]
64. Strukelj, M.; Brais, S.; Quideau, S.A.; Angers, V.A.; Kebli, H.; Drapeau, P.; Oh, S.W. Chemical transformations in downed logs and snags of mixed boreal species during decomposition. *Can. J. For. Res.* **2013**, *43*, 785–798. [[CrossRef](#)]
65. Virzo De Santo, A.; De Marco, A.; Fierro, A.; Berg, B.; Rutigliano, F.A. Factors regulating litter mass loss and lignin degradation in late decomposition stages. *Plant Soil* **2009**, *318*, 217–228. [[CrossRef](#)]
66. Berg, B.; Ekbohm, G. Nitrogen Immobilization in Decomposing Needle Litter at Variable Carbon: Nitrogen Ratios. *Ecology* **1983**, *64*, 63–67. [[CrossRef](#)]

