



RESEARCH ARTICLE

How temperature and aridity drive lignin decomposition along a latitudinal transect in western Siberia

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Funding information

Austrian Science Fund, Grant/Award Number: FWF - I370-B17; German Federal Ministry of Education and Research, Grant/Award Number: 03F0616A; Project 911 of Vietnamese Education

Abstract

Climate change drives a northward shift of biomes in high-latitude regions. This might have consequences on the decomposition of plant litter entering the soil, including its lignin component, which is one of the most abundant components of vascular plants. In order to elucidate the combined effect of climate and soil characteristics on the decomposition pattern of lignin, we investigated lignin contents and its degree of oxidative decomposition within soil profiles along a climo-sequence in western Siberia. Soil samples were collected from organic topsoil to mineral subsoil at six sites along a 1500-km latitudinal transect, stretching from tundra, through taiga and forest steppe to typical steppe. The stage of lignin degradation, as mirrored by decreasing organic carbon-normalized lignin contents and increasing oxidative alteration of the remnant lignin (acid-to-aldehyde ratios of vanillyl- and syringyl-units [(Ac/Al)_V and (Ac/Al)_S]) within soil horizons, increased from tundra to forest steppe and then decreased to the steppe. Principal component analysis, involving also climatic conditions such as mean annual temperature and aridity index, showed that the different states of lignin degradation between horizons related well to the activity of phenoloxidases and peroxidases, enzymes involved in lignin depolymerization that are produced primarily by fungi and less importantly by bacteria. The low microbial lignin decomposition in the tundra was likely due to low temperature and high soil moisture, which do not favour the fungi. Increasing temperature and decreasing soil moisture, facilitating a higher abundance of fungi, led to increased fungal lignin decomposition towards the forest-steppe biome, while drought and high pH might be responsible for the reduced lignin decomposition in the steppe. We infer that a shift of biomes to the north, driven by climate change, might promote lignin decomposition in the northern parts, whereas in the south a further retardation might be likely.

KEYWORDS

climate change, latitudinal gradient, lignin degradation, Siberian soil, soil moisture, temperature, vegetation

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1 | INTRODUCTION

Most biomes on Earth are affected by global warming (Dillon et al., 2010; Pereira et al., 2010), potentially altering the carbon balance between terrestrial ecosystems and the atmosphere (Bond-Lamberty & Thomson, 2010). Expected changes include a shift of biomes particularly at high latitudes (Jiang et al., 2012; Schepaschenko et al., 2013), likely leading to a northward greenness expansion. This will increase the input of aboveground and belowground litter to soils, modify the litter chemical composition and alter the microbial community composition and activity (Grosse et al., 2011). Likewise, changing environmental conditions such as temperature and precipitation may affect soil organic matter (SOM) decomposition and stabilization, with a direct impact on the release of greenhouse gases to the atmosphere (Conant et al., 2011; Grosse et al., 2011; McGuire et al., 2006; Schepaschenko et al., 2013).

Lignin is the second most important plant constituent, entering the soil via aboveground plant litter and roots, and is considered to play an important role in controlling litter decomposition (Hobbie, 1996; Hobbie et al., 2006). Lignin structurally comprises three different monolignols, vanillyl (V), syringyl (S) and cinnamyl (C), and has long been thought to be more stable against microbial decomposition than other major components of plant litter, that is, cellulosic and noncellulosic polysaccharides and proteins (Haider, 1992; Martin et al., 1980). Whereas gymnosperms are dominated by V units, angiosperms are richer in S units and grasses in C units (Hedges & Mann, 1979; Kögel-Knabner et al., 1988). The concentration of the V + S + C units (VSC) varies between different plant taxa and decreases in the order coniferous trees (Raich et al., 2007; Sterjiades & Erikson, 1993), deciduous trees (Devi & Yadava, 2007; Vivanco & Austin, 2008), shrubs (Laishram & Yadava, 1988) and graminoids, mosses and lichens (Dao et al., 2018; Winterfeld et al., 2015).

The best understood mechanism for lignin degradation is associated with fungi, particularly white-rot fungi such as basidiomycetes (Haider, 1986; Kirk et al., 1976). However, bacteria are also known to potentially degrade lignin such as alphaproteobacteria, gammaproteobacteria and actinomycetes (Bugg et al., 2011), with the best-characterized bacterium being *Streptomyces viridosporus* (Ramachandra et al., 1988). In soil, lignin decomposition is generally performed by biologically mediated, oxidative reactions which use free oxygen or ferric iron-bearing minerals as terminal electron acceptors for environments lacking oxygen (Patzner et al., 2020; Peng et al., 2008).

Highlights

- Lack of lignin contribution to soil organic matter and its degradation in different Siberian biomes.
- The dependency of lignin decomposition predicts the fate of lignin under climate warming.
- Climate warming accelerates lignin degradation at high latitude, while in the south it is likely retarded.
- Lignin alteration with climate change has impacted on long-term development of soil carbon stock.

Temperature frequently affects turnover rates of SOM (Conant et al., 2011; Davidson & Janssens, 2006) by generally following three basic theories of decomposition kinetics: (1) when substrate availability and enzyme activity do not constrain reaction rates, decomposition rates increase with temperature (Arrhenius, 1889), (2) increases in decomposition rates with warming temperature should be greatest at cold temperatures (Lloyd & Taylor, 1994) and (3) organic substrates with high activation energies (i.e., slow rates) experience greater proportional increases in decomposition with increasing temperature than those with low activation energy (Davidson & Janssens, 2006). For example, an increase of 2°C has been suggested to accelerate the decomposition of chemically recalcitrant carbon by 21%, compared with only 10% for chemically labile carbon (Davidson & Janssens, 2006). As lignin has a high activation energy, it might be strongly affected by temperature changes, especially in cold climates. Furthermore, soil temperature affects lignin decomposition indirectly by controlling substrate availability for microorganisms as lignin decomposition is a co-metabolic process (Conant et al., 2011). Warming can also promote plant root exudation and generally increase labile SOM forms (Yin et al., 2013), which in turn can accelerate the degradation of old and recalcitrant SOM in high-latitude soils (Keuper et al., 2020; Mau et al., 2018; Wild et al., 2016).

In addition to temperature, soil moisture is one of the most important abiotic variables controlling SOM decomposition (Lawrence et al., 2015; Oechel et al., 1998; Shaver et al., 2006). Warming and drying of wet sedge tundra soils lead to higher soil respiration rates than warming alone (Natali et al., 2015; Oberbauer et al., 2007). In general, moisture affects the quantity and activity of microorganisms and their enzymes through controlling the substrate diffusion and O₂ supply and may also destabilize SOM

especially under reductive conditions (Patzner et al., 2020). On the other hand, long-term soil drought may slow down the rate of SOM mineralization by reducing microbial biomass and activity (Tulina et al., 2009). Several studies, for example, indicated that microbial respiration increases with soil water content from the dry state to normal moisture but decreases if water content further increases (Edwards, 1975; Kowalenko et al., 1978; Wu et al., 2006).

Many studies of lignin in temperate and tropical soils indicated decreasing OC-normalized lignin contents and increasing acid-to-aldehyde ratios of V and S units [(Ac/Al)_V and (Ac/Al)_S] with soil depth as a result of continuous degradation of lignin (Rumpel et al., 2002; Wang et al., 2018). In some cases, lignin has been shown to preferentially accumulate in the subsoil, either due to input of fresh root litter (Angst et al., 2016), low microbial decomposition (Bourdon et al., 2000; Dao et al., 2018; Tareq et al., 2004), or by sorption to reactive mineral surfaces (K. Kaiser & Zech, 1997; Klotzbücher et al., 2016). Soil pH additionally exerts a control on lignin degradation, with an optimal pH for lignin degrading-fungi around 5 and for lignin degradation by *Streptomyces* around 9.5 (reviewed by Thevenot et al., 2010).

Uncertainty remains regarding the interplay between the varying controls on lignin degradation in soil and on the contribution of lignin to SOM in different biomes and soil depths. Here, we investigated the dependency of lignin decomposition on biotic and abiotic soil parameters under natural conditions. To that end, we used a 1500 km long latitudinal bioclimatic transect in western Siberia, stretching from the arctic tundra to the steppe biome. The contents of lignin-derived phenols and their degree of oxidative degradation at different depths of soil profiles along the climosequence were assessed by using the CuO oxidation method. We hypothesized that lignin decomposition along the climosequence is varied across the gradient of temperature and soil moisture. In addition to the direct temperature and moisture effects, we expect the impact on lignin decomposition to be indirect as climatic driving factors are affecting soil parameters, such as litter quality, pH, enzyme composition and activity and microbial community. To disentangle direct and indirect effects of climate parameters on soil lignin degradation along the climosequence, statistical analysis principle component analysis (PCA) and structural equation modelling (SEM) were conducted. For that, we used climatic parameters that is, temperature and aridity index, dominating vegetation, soil pH and C and N availability as assessed by soil C/N ratio, phenoloxidase and peroxidase activities and phospholipid fatty acid (PLFA) patterns as a proxy for bacterial and fungal abundance.

2 | MATERIALS AND METHODS

2.1 | Sampling sites

Soil samples were collected from six biomes along a 1500-km latitudinal transect (67°16'N to 54°41'N) in western Siberia, including tundra, northern taiga, middle taiga and southern taiga, forest steppe and typical steppe (Figure 1). Mean annual temperature (MAT) increased southward from -7.6 to 1.0°C, while mean annual precipitation (MAP) was highest in the middle taiga (438 mm) and lowest in the steppe (309 mm) (Stolbovoi & McCallum, 2002; Table 1). Concurrently, the length of the growing season with daily mean temperatures above 5°C increased towards the southern biomes. Dryness of biome, expressed as aridity index and defined as the ratio of potential evaporation to precipitation (reviewed by Stadler, 2005; Walton, 1969), increased from north (0.44 in tundra) to south (1.30 in steppe) (Schnecker et al., 2015). Dominant vegetation varied among biomes, that is, tundra was characterized by shrubs and lichens, taiga by coniferous trees, the forest steppe was richer in deciduous trees and herbaceous plants, and the steppe showed abundant herbaceous perennials (Table 1).

Soils were sampled in August 2012 during the late growing season at the respective sites. At each site, three replicate soil pits were sampled, in which dominant soil horizons were collected. Soil horizons were designated according to World Reference Base for Soil Resources (IUSS Working Group World Reference Base, 2015). Following Wild et al. (2015), the O and OA horizons were referred to as organic topsoil, the A, AE and EA horizons as mineral topsoil, and the E, B and BC horizons as mineral subsoil (Table 1). Directly after sampling, living plant roots were manually removed, and soil samples were sieved to <2 mm, except for the tundra soil, where samples were too moist for sieving and instead homogenized by hand.

2.2 | Lignin analysis

Concentrations of lignin-derived phenols and their degree of oxidative alteration in soil samples were determined using the alkaline CuO oxidation following the method of Hedges and Ertel (1982) with modifications by Kögel and Bochter (1985). In brief, lignin-derived phenols were released by oxidation with CuO in the presence of [Fe(NH₄)₂(SO₄)₂ × 6H₂O], glucose and 2 M NaOH at 170°C for 3 h. The lignin-derived monomers were purified using a conditioned C₁₈ column and converted to trimethylsilyl (TMS) derivatives by reaction with (N,O-bis-(trimethylsilyl)-trifluoroacetamide) (BSTFA) in pyridine. Thereafter, derivatized-lignin monomers were

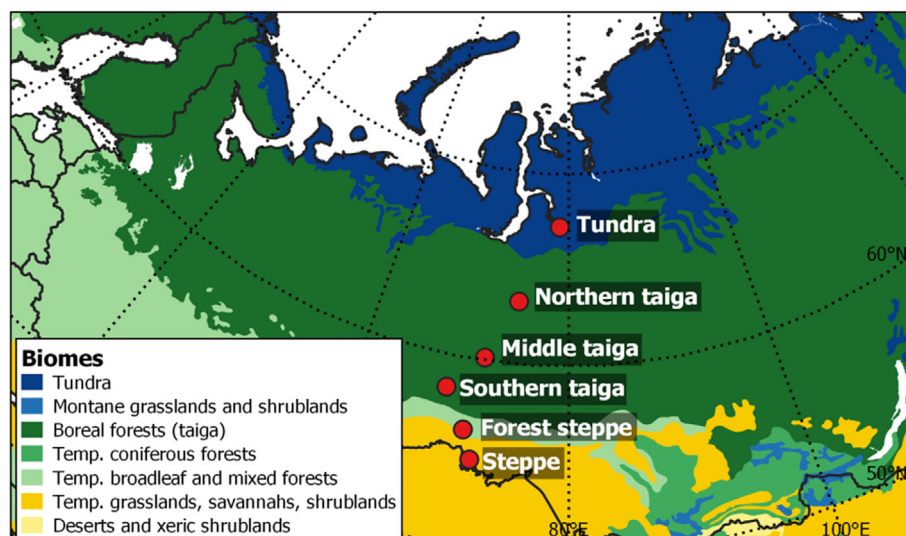


FIGURE 1 Map of sampling sites along the bioclimatic transect in western Siberia.

identified and quantified using gas chromatography–mass spectrometry (450-GC, ion trap 220MS Varian, Palo Alto, CA, USA). Ethylvanillin was used as recovery standard, and added prior to the CuO-oxidation, while phenylacetic acid was used as an internal standard, and added prior to the derivatization. Monomeric lignin-derived phenols were vanillin, acetovanillone, vanillic acid, syringaldehyde, acetosyringone, syringic acid, ferulic acid and *p*-coumaric acid. Vanillyl (V) and syringyl (S) units were calculated as the sum of their aldehyde, ketone and carboxylic acid forms and cinnamyl units (C) are the sum of ferulic acid and *p*-coumaric acid. The $(Ac/Al)_V$ and $(Ac/Al)_S$ ratios were used to assess the degree of lignin alteration (Hedges & Ertel, 1982). The concentration of total lignin was defined as the sum of the eight lignin-derived phenols (VSC) normalized to the soil dry weight ($g\ VSC\ kg^{-1}\ soil$) or normalized to the organic carbon (OC) content of the soil and the C content of the individual lignin-derived phenols ($g\ VSC-C\ kg^{-1}\ OC$). While the former informs on storage of lignin-derived phenols, the latter is suitable to assess the relative enrichment or depletion of lignin-derived phenols during SOM transformation with increasing soil depth (Kögel-Knabner, 1993).

2.3 | Soil parameters

The data on soil pH, OC, total nitrogen (TN) content and the $\delta^{13}C$ value of SOM were taken from Wild et al. (2015) and data of phenoloxidase and peroxidase activity and the bacteria/fungi ratio of the microbial community from Schneckner et al. (2015). The pH was determined potentiometrically using 1 M KCl extracts. Organic C and TN contents as well as the $\delta^{13}C$ value were analysed by elemental analysis-isotope ratio mass spectrometry (EA-IRMS), consisting of a Carlo Erba EA 1110 elemental analyser,

coupled to a Finnigan MAT DeltaPlus IRMS with a Finnigan MAT ConFlo II Interface (Thermo Fisher Scientific, Waltham, MA, USA). Mineral topsoil and subsoil at both forest steppe sites, and all horizons of the steppe site, contained traces of carbonate, which were removed by acidification with HCl before EA-IRMS analysis (Prommer et al., 2014). The C/N ratios of soil samples were calculated on a mass basis between OC and TN. Phenoloxidase activities were measured using L-3,4-dihydroxyphenylalanine (DOPA) as substrate in a photometric assay (Schneckner et al., 2015). Phospholipid fatty acids were determined according to Frostegård et al. (1991) with the modification by C. Kaiser et al. (2010). The bacteria/fungi ratio of the microbial community was estimated by the ratios of PLFAs assigned to bacteria and fungi (for more details see Schneckner et al., 2015).

2.4 | Statistics

One-way ANOVA followed by Tukey's HSD post hoc test was used to test for significant differences in lignin-derived phenol contents and indicators of oxidative lignin alteration between sites and horizons at a significance level of $p \leq 0.05$. Two-way ANOVA was used to test the effect of site and horizon and their interactions. All variables were tested for normal distribution and log transformed if needed. The strength of correlation between parameters was calculated with the Pearson correlation coefficient. Mean differences between the upper and lower horizons were calculated for OC-normalized lignin contents as well as for $(Ac/Al)_V$ ratios in order to describe their relative changes within the soil profiles. Principal component analysis (PCA) and structural equation modelling (SEM) were used to test for relationships between the degree of lignin degradation at different depths

TABLE 1 Characterization of sampling sites along the bioclimatic transect in western Siberia.

Site	Coordinates	MAT (°C)	MAP mm	Aridity index	Dominant plant species	Soil type	Organic topsoil		Mineral topsoil		Mineral subsoil	
							Horizon	Depth (cm)	Horizon	Depth (cm)	Horizon	Depth (cm)
Tundra	67°16'N 78°50'E	-7.6	392	1.3	<i>Betula nana</i> , <i>Cladonia</i> spp.	Turbic Cryosol	O	0-6	A	2-13	Bg, BCg	6-57
Northern taiga	63°17'N 74°32'E	-4.6	430	1.06	<i>Picea obovata</i> , <i>Larix</i> <i>sibirica</i>	Histic Podzol	Oi, Oe	0-22	AE, EA	8-30	Bg	14-47
Middle taiga	60°09'N 71°43'E	-2.2	438	0.89	<i>Abies sibirica</i> , <i>Picea</i> <i>obovata</i>	Endogleyic Regosol	Oi	0-6	A, AE, EA	6-14	E, EA	12-55
Southern taiga	58°18'N 68°35'E	-0.5	396	0.71	<i>Picea obovata</i> , <i>Abies</i> <i>sibirica</i>	Albic Podzol	Oi	0-7	A, AE	4-18	E, EA	15-59
Forest steppe	56°14'N 70°43'E	0.7	340	0.53	<i>Populus tremula</i> , <i>Betula</i> <i>pendula</i> , <i>Calamagrostis</i> <i>epigeios</i> , <i>C. arundinacea</i>	Phaeozem	O, Oa	0-10	A	4-46	B, Bt	26-109
Steppe	54°41'N 71°38'E	1.0	309	0.44	<i>Stipa capillata</i> , <i>Festuca</i> <i>valesiaca</i>	Calcic Kastanozem	Oa	0-12	Ak	8-37	Bk	27-109

Note: Aridity index is defined as the ratio of potential evaporation to precipitation and has a threshold for drylands at 0.65 (Maestre et al., 2012). The data were reported by Wild et al. (2015) and Schnecker et al. (2015).

Abbreviations: MAP, mean annual precipitation; MAT, mean annual temperature.

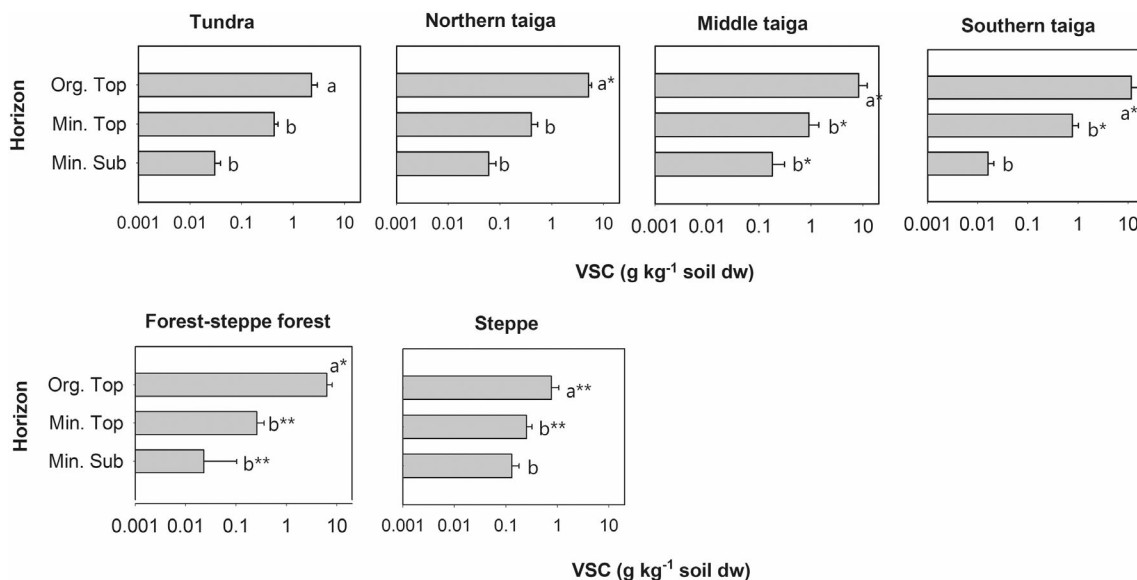


FIGURE 2 Total lignin-derived phenol contents (vanillyl, syringyl and cinnamyl units; VSC) normalized to soil dry weight (dw) within soil profiles at each site (note the log-scale). Error bars represent SDs with $n = 3$. The letters indicate significant differences between horizons of each site, and the symbols * indicate significant differences between sites for each horizon with a significance level $p < 0.05$. Min. Sub, mineral subsoils; Min. Top, mineral topsoils; Org. Top, organic topsoils.

of soil profiles along the climosequence to climatic parameters, soil pH, the C/N ratio of SOM, phenoloxidase and peroxidase activities and PLFA patterns. The PCA was performed using the 'ggbiplot' package in R 4.0.3 in order to reduce the multivariate matrix into a bidimensional space. The SEM analysis was used as a multivariate statistical method to estimate the relative relationships between observed variables, that is, abiotic and abiotic soil parameters, and a latent (unobserved) variable, that is, degree of lignin degradation. The latent variable is a hypothetical construct that involves a confirmatory factor analysis of related measures, that is, the greater degree of lignin degradation is concurring with the increasing ratios of $(Ac/Al)_V$ ($Ac/Al)_S$ and the decreasing VSC-C contents on basis of soil OC. According to Eisenhauer et al. (2015), we hereby distinguish observed variables into exogenous variables (predictor variables that are not influenced by any other variable in the model, i.e., MAT) and endogenous variables (variables that respond to the influence of other variables, that is, soil pH, C/N, enzyme activity, bacteria/fungi ratio). The SEM was run in R 4.0.3 using the 'lavaan' package (Rosseeel, 2012).

3 | RESULTS

3.1 | Lignin patterns in the surface layers

For surface layers, concentrations of lignin-derived phenols were lowest in the steppe (0.7 ± 0.3 g VSC kg⁻¹ soil dw) and highest in the southern taiga (11.5 ± 4.9 g VSC

kg⁻¹ soil dw) (Figure 2). Normalized to OC, lignin-derived phenols ranged from 5.2 ± 2.1 to 14.7 ± 4.5 g VSC-C kg⁻¹ OC (Figure 3), which were lowest for organic topsoil of the tundra and tended to increase towards the south. The $(Ac/Al)_V$ ratios were significantly higher in the organic topsoil of forest steppe and uppermost layer of steppe than those of the northern sites, while the $(Ac/Al)_S$ ratios did not show clear differences between sites (Figure 3). Similarly, S/V ratios were higher in the forest steppe and the steppe than in the taiga and tundra, while no significant difference between sites was observed for the C/V ratios (Figure 3).

3.2 | Lignin patterns in the mineral soils

In the mineral topsoil, lignin-derived phenols accounted for 0.2 ± 0.01 to 0.9 ± 0.5 g VSC kg⁻¹ soil dw (Figure 2). Concentrations were highest in the middle and southern taiga, and lowest in the steppe. Mineral subsoil horizons exhibited 0.03 ± 0.002 to 0.2 ± 0.1 g VSC kg⁻¹ soil, with lowest contents at the southern taiga and the forest steppe sites (Figure 2). On an OC basis, lignin-derived phenol contents in the mineral topsoil ranged from 5.5 ± 3.4 to 11.6 ± 2.6 g VSC-C kg⁻¹ OC, and were lowest in the forest steppe, while no difference was observed for the other sites (Figure 3). In the mineral subsoil, the lignin-derived phenol contents ranged from 2.7 ± 0.8 to 12.3 ± 6.1 g VSC-C kg⁻¹ OC, with largest values in the steppe (Figure 3). The $(Ac/Al)_V$ of mineral topsoils and subsoils appeared to increase from north to south. Values

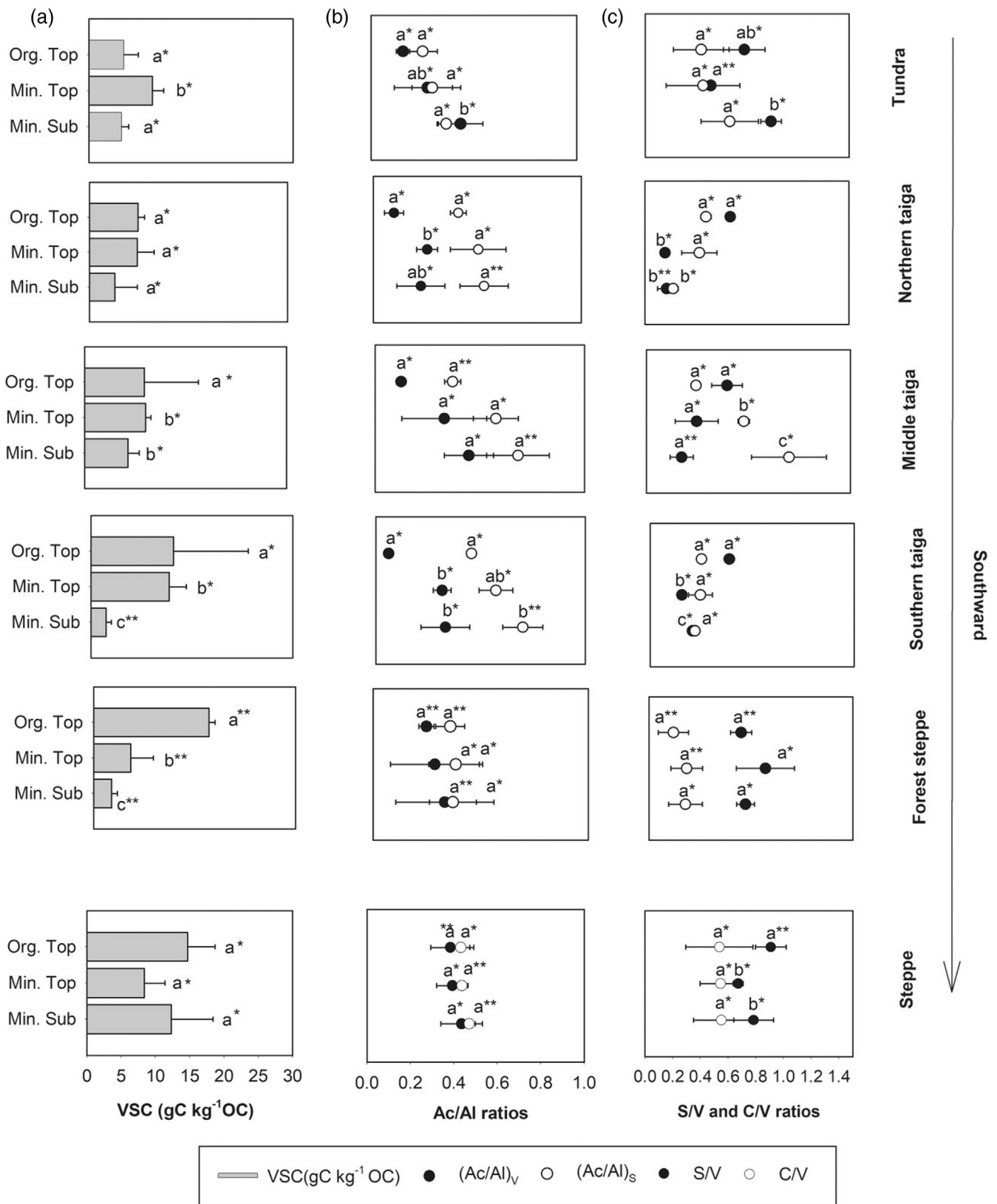


FIGURE 3 Total lignin-derived phenol contents (VSC-C) normalized to organic carbon (OC) within soil profiles at all sampling sites (a) along with ratios of vanillic acid to vanillin [(Ac/Al)_v] and syringic acid to syringaldehyde [(Ac/Al)_s] (b), syringyl units to vanillyl units (S/V) and cinnamyl units to vanillyl units (C/V) (c). Error bars represent SDs with $n = 3$. The letters indicate significant differences between horizons of each site, and the symbols * indicate significant differences between soils for each horizon with a significance level $p < 0.05$. Min. Sub, mineral subsoils; Min. Top, mineral topsoils; Org. Top, organic topsoils.

of $(Ac/Al)_S$ in the mineral topsoil and subsoil exceeded those of $(Ac/Al)_V$ at most sites, and generally increased from the tundra to the southern taiga, and then declined to the steppe (Figure 3).

3.3 | Variability in lignin patterns between horizons

Two-way ANOVA indicates that lignin-derived phenol contents normalized to soil dry weight and OC differed more strongly with soil horizons than with sites (Table 3). Similarly, soil horizons had a larger impact on $(Ac/Al)_V$ than sites. In contrast, $(Ac/Al)_S$ was more variable between sites than soil horizons. Figure 4 reveals the depth-dependent changes of the OC-normalized lignin-derived phenol content and $(Ac/Al)_V$, which are given as the mean difference between the upper and lower horizons. Negative mean differences of OC-normalized lignin-derived phenol contents between the mineral topsoils and the organic topsoils reflect the selective depletion of SOM in lignin from the organic topsoil to the mineral topsoil, except for the tundra (Figure 4a). These differences tended to increase from the northern taiga to the forest steppe, but slightly decreased in the steppe. The difference between mineral subsoils and mineral topsoils was also negative, with the exception of the steppe (Figure 4b). However, they were smaller than those

between organic topsoil and mineral topsoil, and did not show a clear latitudinal trend. Due to cumulative effects, largest mean differences were observed between mineral subsoils and organic topsoils and were strongest at the forest steppe-forest site (Figure 4c).

A positive mean difference of $(Ac/Al)_V$ between mineral topsoils and organic topsoils as well as between mineral subsoils and mineral topsoils was observed, indicating increasing oxidative alteration of lignin with soil depth (Figure 4d–f). However, the mean differences of $(Ac/Al)_V$ between the horizons showed no clear trends between sites. At the basis of the whole soil profile, the largest relative increase of $(Ac/Al)_V$ was observed for the middle and southern taiga sites (Figure 4f). A similar trend was also found for $(Ac/Al)_S$ ratios, but not shown.

3.4 | Lignin patterns in relation to biotic and abiotic parameters

The PCA indicates that soil dw- and OC-normalized contents of lignin-derived phenols were negatively related to $(Ac/Al)_V$ and $(Ac/Al)_S$ (Figure 5). There was a positive relation of $(Ac/Al)_V$ and $(Ac/Al)_S$ with phenoloxidase activities, bacteria/fungi ratios and $\delta^{13}C$. The PCA plot exhibited decreasing VSC contents (both based on soil dry weight and OC) and increasing $(Ac/Al)_V$ and $(Ac/Al)_S$ values with soil depth. Further, the different sites were clustered following the north–south gradient. The SEM reveals a complex impact of climatic and soil parameters on the stage of lignin decomposition (Figure 6). Of the climatic variables, MAT tended to have a positive impact on lignin decomposition. Phenoloxidase activity was significantly positively related to the stage of lignin degradation, and also the bacteria/fungi ratio exerted a positive impact on lignin decomposition (Figure 6). In contrast, the C/N ratio and soil pH showed a negative effect on lignin decomposition in soils along the climosequence.

TABLE 3 F statistics for bi-factorial ANOVA, testing the effects of site and horizon lignin patterns.

Lignin patterns	F values
VSC (g kg ⁻¹ dw)	
Site	7.6***
Horizon	191.8***
Site × Horizon	18.8***
VSC (g VSC-C kg ⁻¹ OC)	
Site	9.3***
Horizon	37.5***
Site × Horizon	6.8***
$(Ac/Al)_V$	
Site	11.0***
Horizon	14.8***
Site × Horizon	2.2*
$(Ac/Al)_S$	
Site	20.9***
Horizon	10.3***
Site × Horizon	1.9*

* $p < 0.05$. *** $p < 0.001$.

4 | DISCUSSION

4.1 | Vegetation effects on organic layer lignin properties

Lignin content and chemical composition in the organic layer samples of the tundra, taiga and forest steppe and the uppermost layer of the steppe reflected the wide variety of vegetation types along our 1500 km latitudinal transect. The average lignin contents of the organic horizons along the climosequence ranged from 3.1 ± 0.6 to 22.9 ± 6.3 g VSC kg⁻¹ OC (Figures 2 and 3), which mirrors well that of 2.3–59.4 g VSC kg⁻¹ OC reported in a

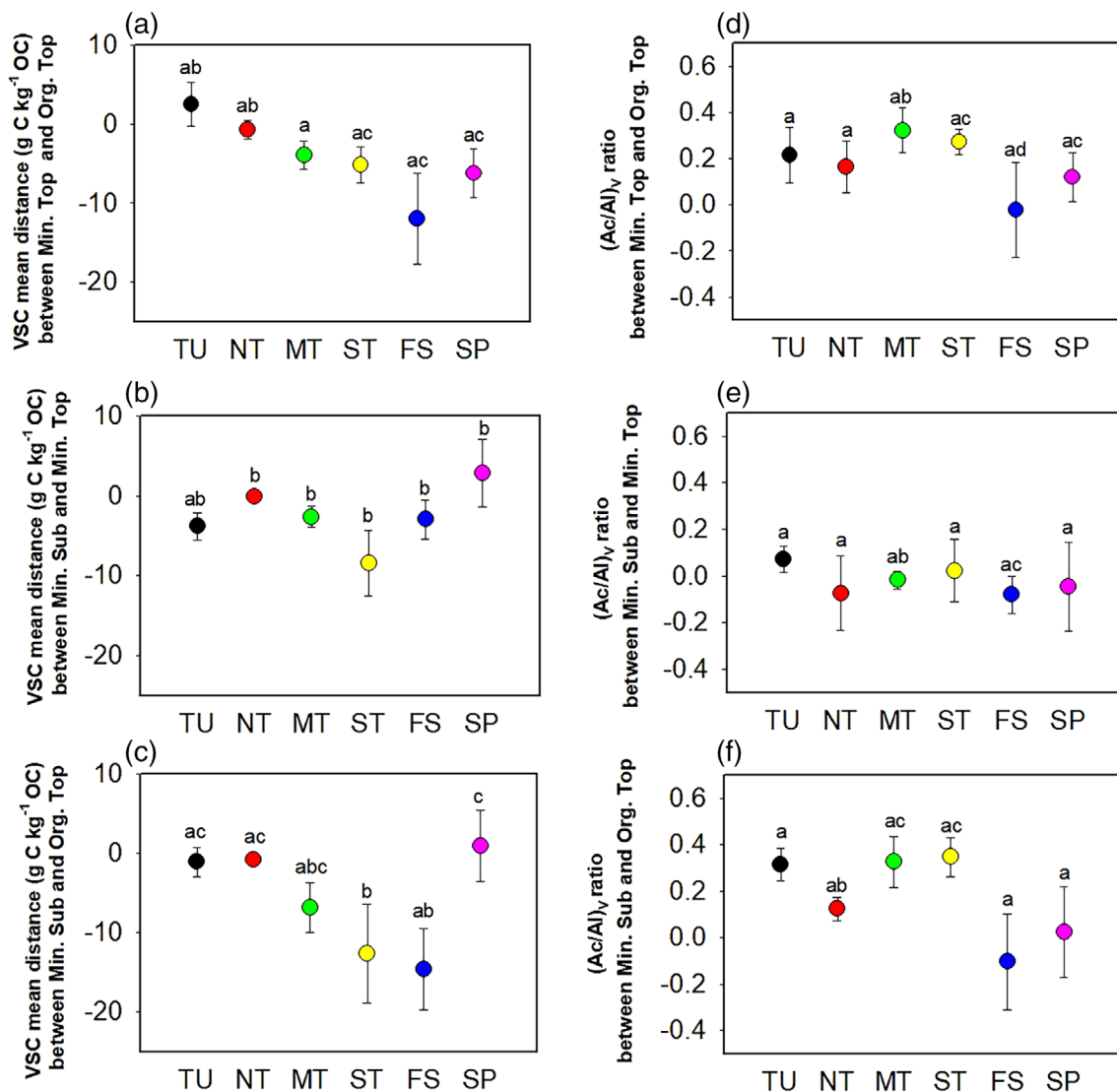


FIGURE 4 Differences between horizons in OC-normalized lignin concentration (a–c) and in (Ac/Al)_v ratios (d–f). Values are the mean difference between the respective shown horizons. Error bars are SDs with $n = 3$. The letters indicate significant differences between sites. FS, forest steppe; Min. Sub, mineral subsoils; Min. Top, mineral topsoils; MT, middle taiga; NT, northern taiga; Org. Top, organic topsoils; SP, steppe; ST, southern taiga; TU, tundra.

review of Thevenot et al. (2010). Tundra vegetation is mainly composed of lichens, mosses and shrubs (Table 1), with only minor production of aboveground litter (Fu et al., 2017). Low litter input rates along with a small contribution of lignin-derived phenols in plant tissues (0.4–20.7 g VSC-C kg⁻¹ OC; Dao et al., 2018) might have contributed to the low lignin contents of tundra organic layers. As compared to mosses, vascular plants were shown to have up to twice as high net biomass production in alpine peatlands (Gerdol et al., 2010) and have higher input of fresh root litter (Schellekens & Buurman, 2011) and living roots (Zeh et al., 2019). The general southward increase in OC-normalized lignin-derived phenols in the organic topsoil from tundra to forest steppe was likely driven by a growing proportion

of vascular plants relative to moss litter, which was in line with a study of a latitudinal transect in boreal Canada (Kohl et al., 2017).

The effect of different vegetation on lignin is also reflected in the relative contribution of the V, S and C units in the organic topsoil. The trend of increasing S/V ratios from the taiga to the forest steppe likely reflects the higher proportion of lignin derived from angiosperms as related to gymnosperms (Hedges & Mann, 1979; Kögel-Knabner et al., 1988). As lignin in grass litter is more enriched in C units (Iiyama et al., 1990; Lam et al., 2001), the C/V ratios in the uppermost layer of the steppe were higher than at the other sites. Hence, the lignin signature in the organic layer reflects the prevailing vegetation along the climosequence.

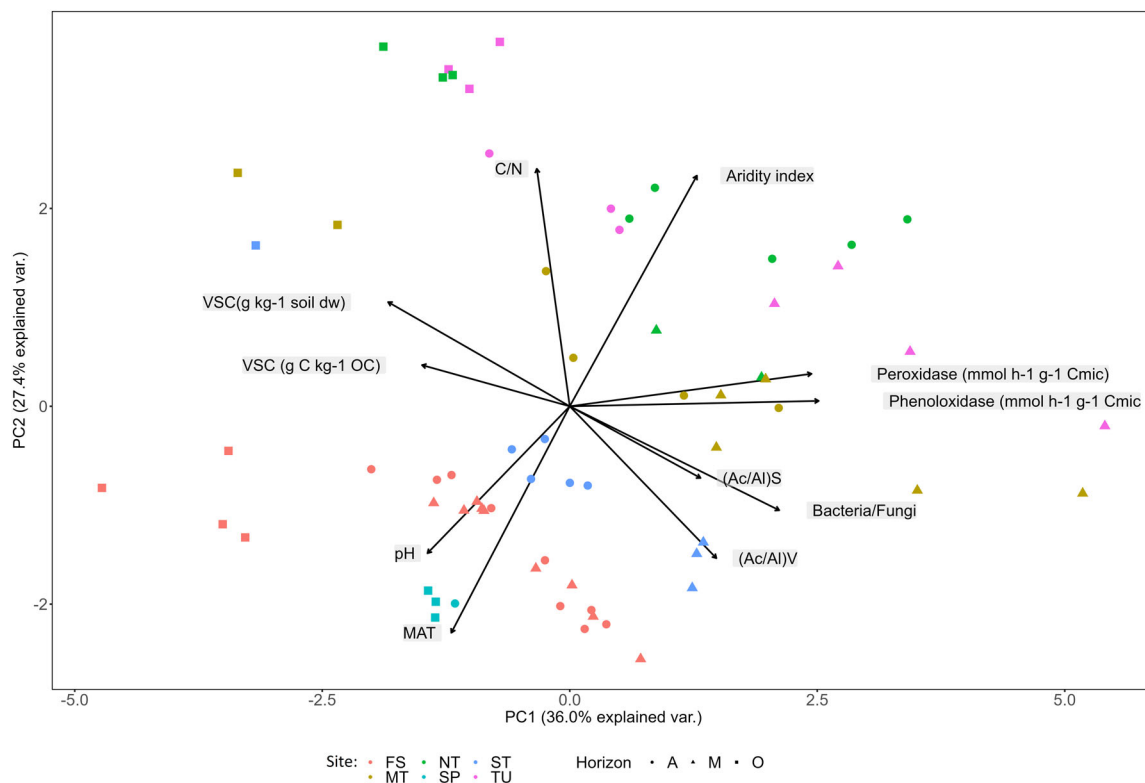


FIGURE 5 Biplot of the first two PCA axes of lignin patterns (VSC, (Ac/Al)_v, (Ac/Al)_s), environmental factors (MAT, aridity index), biological factors (phenoloxidase activity, bacteria/fungi ratio) and soil and SOM factors (soil pH, C/N ratio) for all horizons of all sites. A, mineral topsoils; FS, forest steppe; M, mineral subsoils; MT, middle taiga; NT, northern taiga; O, organic topsoils; SP, steppe; ST, southern taiga; TU, tundra.

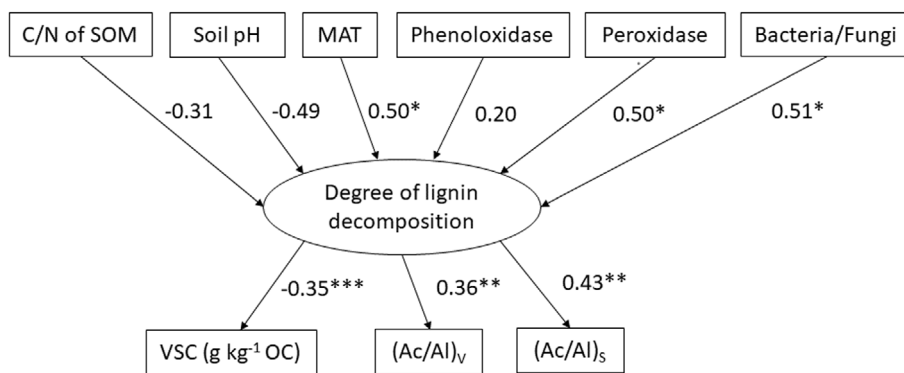


FIGURE 6 Structural equation model showing the effects of mean annual temperature (MAT) and soil parameters (phenoloxidase activity, bacteria/fungi, C/N, pH) on the stage of lignin decomposition which is described by decreasing OC-normalized lignin-derived phenols (VSC-C) and increasing (Ac/Al)_v and (Ac/Al)_s ratios of all studied sites. Numbers on arrows depict standardized path coefficients with their significance indicated as ****p* < 0.001, ***p* < 0.01 and **p* < 0.05.

4.2 | Lignin decomposition dynamics within the soil profiles

Decreasing OC-normalized lignin contents and increasing oxidative alteration of lignin indicate progressing lignin decomposition with soil depth. The sites from the tundra to the forest steppe showed increasing (Ac/Al)_v and

(Ac/Al)_s ratios with soil depth. These climosequences also showed decrease of OC-normalized lignin contents with soil depth, except the tundra. Moreover, the varying mean differences of the oxidative ratios and lignin contents between deeper and upper horizons were more pronounced in the southern taiga and forest steppe than in the northern sites. These findings suggested an increased

degree of lignin decomposition from tundra towards forest steppe. The increasing temperature from the north to south primarily explained the increasing degree of lignin decomposition. According to kinetic theory, SOM decomposition increases with temperature, especially in cold regions (Conant et al., 2011). This finding was supported by a significant relationship between the degree of lignin degradation and MAT as shown in PCA and SEM (Figures 5 and 6). In addition to temperature, soil moisture affects microbial community composition and enzyme activity through managing oxygen availability (Tulina et al., 2009). Because the underlying permafrost impedes subsurface drainage, tundra soils are often wet and the soils become drier to the south with thinner/no permafrost. Consequently, O₂ limitation increased towards the southern biomes. Since lignin-degrading enzymes such as phenoloxidases and peroxidases are oxygen-dependent, lignin decomposition is more pronounced in southern soils with better O₂ supply. Using the same set of samples as this study, Schneckner et al. (2015) showed that the soil microbial community composition and their phenoloxidase and peroxidase activity differed more strongly between soil horizons than between biomes. (Table 2). Similarly, we here found that also the lignin-derived phenol contents and (Ac/Al)_V ratios were more different between horizons rather than sites (Table 3). In comparison between biomes, the bacteria/fungi ratios were likely higher in the tundra than south located biomes corresponding to soil horizons (Table 2). This finding suggested the abundance of fungal community, which was most efficient in lignin degradation, was more pronounced in the southern biomes than in the tundra. Overall, we found the positive relationship between the degree of lignin degradation and the activities of phenoloxidase and peroxidase enzymes (Figures 5 and 6), suggesting that these enzymes were primarily accounted for lignin decomposition. The effect of soil moisture on lignin decomposition was in line with a previous study of Dao et al. (2022) who indicated that lignin appeared to slightly decompose with soil depth in western Siberian tundra, although it was selectively preserved in central and eastern Siberia due to differences in the stage of anaerobiosis. We hence implied that the impact on lignin decomposition to be indirect as climatic driving factors are affecting enzyme composition and activity, and microbial community.

Although the (Ac/Al)_V and (Ac/Al)_S of lignin was increased with soil depth, no trend for VSC contents was observed in the tundra. The weak trend in lignin contents with depth of tundra may be explained by preferential sorption of lignin to mineral surfaces (K. Kaiser et al., 2001; K. Kaiser & Zech, 2000; and as reviewed by Angst et al., 2021) rather than by from plant input. Since tundra is characterized by vegetation with no (e.g., mosses, lichens) or

TABLE 2 Basic soil characteristics of the study sites.

	Tundra			Northern taiga			Middle taiga			Southern taiga			Forest steppe-forest			Steppe		
	Organic topsoil	Mineral subsoil	Mineral topsoil	Organic topsoil	Mineral subsoil	Mineral topsoil	Organic topsoil	Mineral subsoil	Mineral topsoil	Organic topsoil	Mineral subsoil	Mineral topsoil	Organic topsoil	Mineral subsoil	Mineral topsoil	Organic topsoil	Mineral subsoil	Mineral topsoil
OC (g kg ⁻¹ dw)	303.0 (69.30)	28.51 (6.30)	4.22 (1.30)	452.10 (12.00)	37.00 (7.00)	7.10 (2.60)	408.20 (67.80)	63.30 (33.50)	16.70 (8.40)	393.90 (57.30)	43.40 (8.10)	4.70 (0.80)	229.20 (56.10)	35.00 (13.20)	5.60 (0.60)	33.90 (11.30)	20.10 (6.10)	7.20 (1.80)
C/N	31.96 (5.65)	16.00 (1.50)	10.95 (1.57)	34.99 (1.38)	27.35 (4.45)	14.89 (1.07)	23.82 (0.74)	20.52 (4.70)	16.29 (3.81)	26.59 (0.69)	13.96 (1.79)	9.39 (0.47)	15.44 (1.01)	12.96 (0.45)	10.27 (0.65)	10.99 (0.36)	10.84 (0.58)	9.15 (0.40)
δ ¹³ C (‰)	-26.54 (0.46)	-25.69 (0.10)	-24.57 (0.23)	-28.27 (0.46)	-27.13 (0.59)	-25.79 (0.11)	-29.14 (0.32)	-26.94 (0.61)	-26.54 (0.56)	-28.38 (0.53)	-26.80 (0.08)	-25.24 (0.19)	-27.71 (0.20)	-25.98 (0.47)	-25.62 (0.40)	-25.38 (1.13)	-25.09 (0.61)	-24.87 (0.18)
pH	3.73 (0.12)	3.70 (0.08)	3.88 (0.13)	2.80 (0.10)	3.06 (0.11)	3.77 (0.06)	3.67 (0.06)	3.25 (0.10)	3.48 (0.11)	4.23 (0.31)	3.62 (0.16)	3.73 (0.17)	6.37 (0.96)	4.20 (0.12)	4.04 (0.13)	4.59 (0.10)	5.08 (0.11)	7.92 (0.91)
Phenoloxidase (nmol h ⁻¹ g ⁻¹ C _{mic})	1.03 (0.39)	5.32 (2.31)	23.95 (7.29)	1.39 (0.68)	17.11 (9.26)	8.99 (1.93)	0.89 (0.23)	9.44 (5.88)	17.43 (8.15)	1.23 (1.12)	5.02 (0.58)	11.30 (4.27)	0.25 (0.08)	3.86 (1.73)	7.17 (2.18)	1.94 (1.21)	3.47 (0.88)	7.66 (2.13)
Bacteria/Fungi	1.49 (0.59)	1.87 (0.23)	6.04 (2.69)	1.28 (0.08)	3.78 (1.50)	4.82 (0.79)	1.20 (0.41)	3.56 (1.02)	4.65 (0.67)	1.90 (0.08)	3.58 (1.50)	4.17 (0.79)	0.11 (0.06)	4.59 (2.72)	3.79 (1.47)	3.40 (0.07)	2.95 (0.66)	2.58 (0.48)

Note: All values are means with SD in brackets (Wild et al., 2015).

Bacteria/Fungi indicates the ratio of phospholipid fatty acids (PLFA) assigned to bacteria-to-PLFA assigned to fungi according to Schneckner et al. (2015).

shallow roots (Iversen et al., 2015), lignin input from fresh roots into mineral horizons, especially in the mineral subsoil, is restrained and thus hardly can be the reason for the observed lacking decrease in OC-normalized VSC-C contents. On the other hand, the permafrost soil layer impairs fast water drainage, which may support the interaction of dissolved OM with soil minerals (Ostroumov, 2004). In addition, the higher contribution of lignin in mineral topsoil may be due to cryoturbation which causes a mixing of particulate OM (POM) from organic topsoil to mineral topsoil. In line with this finding, Gentsch et al. (2015) showed one-third of POM-C in topsoil of tundra compared to bulk OC. We therefore speculate that cryoturbative processes might also affect 'non-buried' topsoil horizons via incorporation of lignin-containing plant residues.

In the steppe, however, no trend of VSC contents as well as $(Ac/Al)_V$ and $(Ac/Al)_S$ were observed with depth, likely indicating a restrained lignin decomposition in the subsoils, or reflecting the fact that its surface soil layer was quite mineral and that caused a weaker gradient in soil properties than at the other sites. According to Climate classification and dryland subtypes based on aridity index (Middleton & Thomas, 1997), the steppe site was in the range of a semiarid climate (aridity index = 0.44, Table 1), which is characterized by insignificant rainfall and snowmelt. Therefore, steppe soil often remains dry, especially in the subsoil (Monger et al., 2005). Low soil moisture reduces microbial activities in general (Gill & Burke, 2002; Klotzbücher et al., 2016; Liu et al., 2009) and restricts the availability of substrates to microorganisms (Amelung et al., 1999; Moyano et al., 2013), leading to retarded SOM degradation, including that of lignin. Further, slower lignin degradation in subsoil horizons of the steppe could additionally be favoured by the slightly alkaline pH (8.0 ± 1.0 , Table 2), which might impair the activity of lignin-degrading enzymes (reviewed by Thevenot et al., 2010). Hence, both soil moisture and pH might contribute to the lower lignin degradation at the steppe, which is supported by the negative correlations between lignin decomposition and aridity index and pH (Figures 5 and 6). These findings are also consistent with the study of Kayler et al. (2018) who found a faster SOM turnover in southern taiga than in steppe soils.

The C/N ratio of SOM and plant litter inputs is expected to decrease with depth and latitude, that is, from arctic over boreal and temperate to tropical systems (Post et al., 1985; Xu et al., 2013). In line with these studies, the C/N ratios decreased from tundra to forest-steppe, and from organic topsoil to mineral subsoil (Table 2; Wild et al., 2015). The SEM and PCA analyses showed a decreasing state of lignin degradation with increasing C/N ratio of SOM (Figures 5 and 6). The fact that, the C/N ratio is decreasing with increasing SOM

decomposition due to an increasing proportion of microbial residues on the SOM (Hoorman & Islam, 2010). Concurrently, the proportion of plant-derived substances, including lignin, on SOM is decreasing. Hence, with increasing soil depth decreasing C/N ratios go along with increasing lignin degradation (i.e., decreasing VSC contents and increasing $(Ac/Al)_V$ and $(Ac/Al)_S$ ratios). Our findings thus mirror the higher proportion of microbial substances and the concurrent lower proportion of plant-derived substances (i.e., lignin) with soil depth.

5 | CONCLUSIONS

Our study revealed that the pattern of decomposition and preservation of lignin along a climosequence in western Siberia depends on a complex interaction of direct and indirect effects of environmental parameters. In the tundra, lignin decomposition is less decomposed due to frozen soils and anaerobiosis, which are not favouring the fungi, the most efficient lignin decomposer. In mid-latitude soils, the acidic pH and drier soils are preferentially attracting fungi, leading to advanced lignin degradation. In the steppe, limited water, but also high pH, retard lignin degradation. These findings suggest that warmer and drier conditions with climate change could accelerate lignin decomposition at high latitudes. An expansion of the steppe biome towards the southern taiga may in contrast lead to a retardation of lignin decomposition in these areas. Such changes may also have an impact on the overall long-term development of soil organic carbon stocks.

AUTHOR CONTRIBUTIONS

Thao Thi Dao: Writing – original draft; conceptualization; methodology; formal analysis. **Robert Mikutta:** Conceptualization; writing – review and editing; project administration. **Birgit Wild:** Writing – review and editing; project administration. **Leopold Sauheitl:** Methodology; writing – review and editing. **Norman Gentsch:** Writing – review and editing; formal analysis. **Olga Shibistova:** Writing – review and editing. **Jörg Schneckner:** Writing – review and editing. **Nikolay Lashchinskiy:** Writing – review and editing. **Andreas Richter:** Project administration. **Georg Guggenberger:** Project administration; writing – review and editing; conceptualization; supervision.

ACKNOWLEDGEMENTS

The financial support was provided by the German Federal Ministry of Education and Research (03F0616A) within the ERANET EUROPOLAR project CryoCARB. T. T. Dao is grateful for financial support by the Project 911 of Vietnamese Education. A. Richter acknowledges

the financial support of the Austrian Science Fund (FWF – I370-B17). We are grateful to the technical staff of the Institute of Soil Science in Hannover for laboratory assistance and to Susanne K. Woche for comments on the manuscript. Open Access funding enabled and organized by Projekt DEAL.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available on request from the corresponding author. The data are not publicly available due to privacy or ethical restrictions.

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How to cite this article: Dao, T. T., Mikutta, R., Wild, B., Sauheitl, L., Gentsch, N., Shibistova, O., Schneckner, J., Lashchinskiy, N., Richter, A., & Guggenberger, G. (2023). How temperature and aridity drive lignin decomposition along a latitudinal transect in western Siberia. *European Journal of Soil Science*, *74*(5), e13408. <https://doi.org/10.1111/ejss.13408>