



Relationship between the chemical structure of straw and composition of main microbial groups during the decomposition of wheat and maize straws as affected by soil texture

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Abstract

Field decomposition of wheat and maize straws was monitored for 20 months using litterbag method in Calcaric Fluvisol soils with three different textures (sand, sandy loam, and silty clay). Residual straw samples were collected at 0 or after 4, 6, 10, and 20 months of decomposition. The chemical structure of straw was analyzed by solid-state ¹³C nuclear magnetic resonance (¹³C-NMR) spectroscopy, and the composition of main microbial groups was evaluated by phospholipid fatty acid analysis. Regardless of the straw type and soil texture, the straw biomass and C loss increased steadily in the first 10 months and then leveled off in the following 10 months; both the chemical structure of straw and the composition of main microbial groups differed during incubation. During the first 4 months of wheat straw degradation, the decrease in di-O-alkyl and O-alkyl C and the increase in alkyl and N-alkyl/methoxyl C contents were related to the enrichment of fungi (18:1ω9c) and Gram-negative bacteria (18:1ω7c and 16:1ω7c), while the degradation of maize straw was associated with the decrease in the fungal (18:1ω9c) abundance and the increase in the abundance of Gram-negative (18:1ω7c and 16:1ω7c) and Gram-positive (a15:0) bacteria. During the 6–10-month period, the decrease in di-O-alkyl and O-alkyl C and the increase in alkyl, aryl, and carboxyl/amide C contents were related to the enrichment of arbuscular mycorrhizal fungi (AMF) (16:1ω5c) and Gram-negative (cy19:0ω8c) bacteria and the decrease in fungal (18:2ω6,9c) abundance, with AMF playing an important role in the degradation of both straw types. The altered chemical structure of wheat and maize straws had opposite links with fungal abundance during the first 4 months, while alterations occurring during the 6–10-month period mainly depended on the variation in the AMF abundance.

Keywords Wheat straw · Maize straw · ¹³C-NMR · Phospholipid fatty acid · Decomposition dynamics

Introduction

Soil organic carbon (SOC) in agricultural soil is the core of soil fertility (Zech et al. 1997). The SOC sequestration in China's croplands has been largely attributed to higher residue inputs following the large-scale implementation of crop straw/stover return policy since 2000 (Zhao et al. 2018). Therefore,

the addition of crop straw to soil can increase the SOC content by incorporating straw C into soil (Yin et al. 2014; Ghafoor et al. 2017; Shahbaz et al. 2017) and supplying a large amount of nutrients (e.g. N, P, and K) for crop growth (Takahashi et al. 2003; Sun et al. 2019). Research on the mechanisms of straw decomposition in soil has become very important (Carvalho et al. 2009; Bray et al. 2012; Wickings et al. 2012; Xu et al. 2017), and in particular, an understanding of the associations between the chemical structure of straw and microbial community composition can provide insights into these mechanisms (Baumann et al. 2009; Xu et al. 2017).

The chemical structure of residual straw depends on various factors (Baldock and Skjemstad 2000; Baumann et al. 2009; Xu et al. 2017), with the initial litter quality and soil condition being particularly important (Baumann et al. 2009; Mula-Michel and Williams 2013; Li et al. 2015). Baumann et al. (2009) found that the aryl C content increased in vetch (*Vicia sativa* L.) straw and decreased in eucalypt (Tasmanian

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blue gum, *Eucalyptus globulus* Labill) straw after 150 days of decomposition, whereas the aryl C content of wheat (*Triticum aestivum* L.) straw decreased markedly in the first 5 days, followed by a steady increase for the next 140 days. Furthermore, aryl C in black locust (*Robinia pseudoacacia* L.) litter was observed to be a highly decomposable component, whereas it was more recalcitrant in black pine (*Pinus nigra* Arn.) litter (De Marco et al. 2012). Although corn and grass (primarily *Bromus inermis*, Leyss) litter presented similar initial contents of lignin and phenols, the residual corn litter, which accounted for 75–80% of the initial mass, had a higher lignin (47% vs. 28%) and lower phenols (2% vs. 8%) contents than the residual grass litter (Wickings et al. 2012). However, Wang et al. (2012) reported a similar gradual decrease in di-O-alkyl and O-alkyl C contents, accompanied by a continuous increase in alkyl, aromatic, phenolic, and carbonyl C contents with time in both wheat and maize (*Zea mays* L.) straws during a 24-month decomposition period. In addition, soil texture and particularly the clay content, moisture, and temperature conditions also exert strong influence on chemical variation of straw during decomposition via changes in the composition and activity of the decomposer community (Wickings et al. 2012; Mula-Michel and Williams 2013).

Microorganisms are the major decomposers of plant materials (Berg and McClaugherty 2008), and microbial species with diverse metabolic capacities decompose different components to different extents (Romani et al. 2006). Generally, fungi degrade the aromatic structure in lignin via side-chain oxidation and ring opening, resulting in the steady accumulation of carboxyl C (Dijkstra et al. 1998). Bacteria had a lower capacity to degrade lignin and cellulose than fungi (Romani et al. 2006), and Gram-negative bacteria (G^-) are fast-growing r-strategists degrading labile substrates (Derrien et al. 2014). The composition of the decomposing microbial community is strongly affected by the initial litter quality (Wilkinson et al. 2002; Bray et al. 2012; Wickings et al. 2012) and soil conditions (Mula-Michel and Williams 2013; Jung et al. 2014). Gram-negative bacteria tend to dominate in litter with a higher N content than cellulose and lignin content, whereas Gram-positive bacteria (G^+) and fungi prefer cellulose and lignin (Bray et al. 2012). Baumann et al. (2009) found that the microbial community composition differed significantly during the 150-day degradation period of wheat, vetch, and eucalypt litters. Generally, the soil texture influences the soil environment by changing the distribution and location of space, and these factors will, in turn, change the growth and activity of microbial communities (Scott et al. 1996; Mula-Michel and Williams 2013). Mula-Michel and Williams (2013) showed that the residual switchgrass (*Panicum virgatum* L.) and rice (*Oryza sativa* L.) associated bacterial communities were separated into two distinct groups according to the soil type after 110 days of decomposition.

Microbial succession can occur during litter decomposition (Moore-Kucera and Dick 2008; Poll et al. 2008; Marschner et al. 2011). For example, during the decomposition of wheat straw, the bacterial fatty acids peaked on days 2 and 4, while the fungal fatty acids peaked on day 15 (Marschner et al. 2011). In contrast, Bray et al. (2012) demonstrated an increase in G^+ and G^- bacterial abundances and a decrease in fungal abundance during the degradation of 10 different straw types over an 8-month decomposition period.

The succession of decomposer community was associated with the change in the chemical structure of straw during the decomposition (Baumann et al. 2009; Xu et al. 2017). Baumann et al. (2009) showed that the microbial community composition depended on the aryl C content of wheat and vetch straws and the O-alkyl C content of eucalypt straw at the end of decomposition. Xu et al. (2017) established that the abundance of G^- bacteria and actinobacteria was positively correlated with di-O-alkyl and O-alkyl C contents and negatively correlated with alkyl, methoxyl, aromatic, and carbonyl C contents at the end of degradation of *Pinus massoniana* needles. However, both these studies did not investigate the dynamic patterns during degradation.

We hypothesized that the relationships between the chemical structure of straw and the composition of main microbial groups can change during straw decomposition. The North China Plain (NCP) is one of the major agricultural production areas in China, and the representative soil in this area is a Calcaric Fluvisol (FAO 1998), whose texture can be coarse or finer (Xia et al. 2015). In the present study, Calcaric Fluvisol soils with three different textures (sand, sandy loam, and silty clay) and wheat and maize (the typical cropping systems of the NCP) straws were employed. We monitored the composition of main microbial groups and the chemical structure of straw during the 20-month decomposition period. The objectives of this study were to (1) investigate the changes in the chemical structure of straw and the evolution of the main microbial groups with time and (2) study how the relationship between the chemical structure of straw and the composition of the main microbial groups is affected by straw quality, soil texture, and decomposition period.

Materials and methods

Study site

The study was conducted in the Fengqiu Agro-ecological Experimental Station of the Chinese Academy of Sciences, which is located in Pandian, Fengqiu Country, Henan Province, China (114° 34' E, 35° 01' N), a site representative of the NCP. The site has a typical monsoon climate with annual average temperatures of 13.9 °C and an annual average precipitation of 597 mm, 57% of which occurs from July to

September. The winter wheat was grown from October to May and summer maize from June to September, each year. The soil in the NCP was derived from alluvial sediments of the Yellow River and is classified as Calcaric Fluvisol according to the FAO (1998).

Experimental setup and sampling

In 1992, three types of Calcaric Fluvisol were collected in Huangling (114° 42' E, 34° 58' N), Pandian (114° 34' E, 35° 01' N), and Huangde (114° 25' E, 35° 11' N), respectively. They were sand (Sd), sandy loam (SdL), and silty clay (StC), respectively. The soils were then transferred to the study site and placed in the experimental plots layer by layer (20 cm per layer) according to the original layer sequence. Each experimental plot measured 1.5 m wide × 2 m long × 0.6 m deep and was separated by cement banks (60 cm deep and 10 cm above the soil surface). Three replicates of each soil textural type were used, with nine plots in total. The plots were arranged in a randomized complete block design.

The straw decomposition study was initiated in October 2012, when the winter wheat was sown. Prior to 2012, all the experimental plots had been under the cropping of winter wheat and summer maize for more than 5 years. Some of the soil properties determined before the decomposition experiment are listed in Table 1.

Wheat and maize straws were placed in litterbags (10 cm wide × 12.5 cm long) made of double-layer nylon mesh; bags were buried in soil on December 4, 2012. The mesh size of the litterbags was 0.074 mm, which would prevent the mixing of the straw residuals with the surroundings while allowing access of water and microorganisms (Wang et al. 2012). Each litterbag contained either 13.67 g oven-dried wheat straw or 13.31 g oven-dried maize straw; the straw was cut into 2 cm pieces. In the NCP, crop straws are usually returned back to the field on harvest, followed by mixing with the topsoil (0–15 cm) mechanically. To mimic the field condition, the litterbags were inserted vertically at 15 cm depth in each plot and were covered with a 5-cm layer of soil on the surface. Each

plot received 5 litterbags containing wheat straw or maize straw, this resulted in a total of 90 litterbags; only 72 litterbags were used in the present study (2 residue types × 3 replicates × 3 soil textures × 4 sampling times). The wheat straw contained the following: 450.1 g C kg⁻¹, 8.41 g N kg⁻¹, 0.58 g P kg⁻¹, and 29.49 g K kg⁻¹. The maize straw contained the following: 469.1 g C kg⁻¹, 8.61 g N kg⁻¹, 0.96 g P kg⁻¹, and 11.93 g K kg⁻¹.

Three wheat straw and 3 maize straw bags were sampled randomly from three plots of each soil on April 4, 2013 (4 months), June 4, 2013 (6 months), October 4, 2013 (10 months), and August 4, 2014 (20 months). After each sampling, the adhered soil was gently removed, and each residual straw sample was divided into 2 parts after weighing. The first part was oven-dried (50 °C) and ground to pass through a 0.15-mm sieve for chemical analysis. The other moist part was stored at –20 °C for up to 2 weeks before analyses of the main microbial groups. The biomass weight was expressed as an oven-dried (50 °C) weight of the residual straw contained in litterbags following each sampling, and the C concentration of residual straw was determined by dichromate oxidation (Page et al. 1982). The percentage of biomass or C loss of straw in the litterbag after a certain decomposition time was calculated using the following equation: Biomass or C loss (%) = $(M_0 - M_t) / M_0 \times 100$, where M_0 is the initial mass of biomass or C of the straw, M_t is the residual mass of biomass or C of the straw at time t , and t (month) is the decomposition time from straw burial to the sampling time.

Nuclear magnetic resonance spectroscopy

Chemical composition of the residues was determined with solid-state ¹³C nuclear magnetic resonance spectroscopy (NMR) by employing a Bruker AVANCE III 400 spectrometer (Bruker BioSpin, Rheinstetten, Germany) operating at a ¹³C resonance frequency of 100.6 MHz. The samples were pressed into a 4-mm zirconia rotor and spun at 14 kHz. A contact time of 0.5 s and a relaxation delay of 1500 μs including a ramp-contact and spinal 64 decoupling pulse program

Table 1 Basic physical and chemical properties of the Calcaric Fluvisol soil at the start of the straw decomposition experiment in 2012

	Huangling (Sand)	Pandian (Sandy loam)	Huangde (Silty clay)
pH (H ₂ O)	8.68 ± 0.02 a	8.51 ± 0.01 b	8.51 ± 0.01 b
Soil organic carbon (g kg ⁻¹)	3.22 ± 0.25 c	5.65 ± 0.45 b	7.73 ± 0.22 a
Total N (g kg ⁻¹)	0.35 ± 0.06 c	0.62 ± 0.06 b	0.94 ± 0.02 a
Total P (g kg ⁻¹)	0.87 ± 0.01 b	1.08 ± 0.02 a	1.10 ± 0.01 a
Total K (g kg ⁻¹)	18.29 ± 0.13 b	18.03 ± 0.05 c	20.78 ± 0.05 a
Sand (2–0.02 mm) % (wt)	85.91 ± 0.01 a	64.65 ± 0.01 b	6.75 ± 0.04 c
Silt (0.02–0.002 mm) % (wt)	9.50 ± 0.01 c	20.84 ± 0.00 b	54.23 ± 0.04 a
Clay (<0.002 mm) % (wt)	4.59 ± 0.00 c	14.52 ± 0.01 b	39.02 ± 0.04 a

Lowercase letters refer to the comparison within the three soils at $P < 0.05$

were used. The spectra were recorded as the sum of 5000 scans and were calibrated using the methine C atoms of adamantane as an external standard at 29.47 ppm.

Each of the ^{13}C NMR spectra was divided into eight chemical shift regions assigned to different C functional groups: alkyl C (0–45 ppm), N-alkyl/methoxyl C (45–60 ppm), O-alkyl C (60–90 ppm), di-O-alkyl C (90–110 ppm), aryl C (110–145 ppm), O-aryl C (145–160 ppm), carboxyl/amide C (160–190 ppm), and ketone/aldehyde C (190–220 ppm) (Mathers et al. 2007; Baumann et al. 2009). The relative contents of different C functional groups were obtained by integrating the signal intensities within various chemical shift regions and then expressed as percentages of the total area (0–220 ppm).

PLFA analysis

The composition of main microbial groups was determined using Phospholipid fatty acid (PLFA) analysis. Extraction of PLFA was carried out as described by Frostegård et al. (1993). Moist straw (equivalent to 0.5 g oven-dried) was extracted for 2 h with 15 ml of a chloroform–methanol–phosphate buffer mixture (1:2:0.8, pH 7.0). The phospholipids were separated from glycolipids and neutral lipids using silicic acid-bonded solid-phase extraction columns by sequential leaching with chloroform, acetone, and methanol. Phospholipids were saponified and methylated to fatty acid methyl esters (FAMES) under N_2 at 37 °C and then were dissolved in hexane containing a 19:0 (methyl nonadecanoate fatty acid) FAME standard. The resulting fatty acid methyl esters (FAMES) were analyzed with an Agilent 6850 gas chromatograph (GC) equipped with an Agilent Ultra (25%-phenyl)-methyl siloxane column (25 m \times 200 μm i.d. \times 0.33 μm film thickness; Agilent Inc., Santa Clara, CA, USA).

The following PLFAs were used as indicators for specific microbial groups: 12:0, 14:0, 16:0, 17:0, 18:0, and 20:0 for bacteria (Fontaine et al. 2011; Xu et al. 2017); i14:0, i15:0, a15:0, i16:0, a16:0, i17:0, a17:0, and i19:0 for G^+ bacteria (Kulmatiski 2011; Bland et al. 2012); 16:1 ω 9c, 17:1 ω 8c, 16:1 ω 7c, 18:1 ω 7c, cy17:0, cy19:0 ω 8c, and i17:0 3OH for G^- bacteria (Bray et al. 2012; Zhang et al. 2014); 18:1 ω 9c, 18:2 ω 6,9c, and 18:3 ω 6,9,12c for fungi, and 16:1 ω 5c for arbuscular mycorrhizal fungi (AMF) (Marschner et al. 2011; Wang et al. 2014); and 10Me16:0, 10Me17:0, and 10Me18:0 for actinomycetes (Ding et al. 2009; Gomez et al. 2014). The amount of an individual PLFA was expressed as $\mu\text{g g residue}^{-1}$. The ratios of G^+ to G^- (G^+/G^-) and of fungi to bacteria biomass (F/B) were also calculated.

Statistical analysis

All data were analyzed using the Kolmogorov–Smirnov test and the Levene statistic for normality and homogeneity of

variance. Variables not meeting normality assumptions, including biomass and C loss, ketone/aldehyde C, carboxyl/amide C, O-aryl C, di-O-alkyl C, and O-alkyl C contents, were log-transformed. We performed repeated measures analysis of variance (ANOVA) to analyze the impact of soil texture and straw type on the biomass and C loss, C functional groups, and microbial indicators. Meanwhile, significant differences in the variables among sampling times were subjected to one-way ANOVA with an LSD test. Relationships between the C functional groups and the PLFA biomarkers were determined by Pearson's correlation analysis. All these statistical analyses were performed using IBM SPSS Statistic v19.0 software with significant differences accepted at $P < 0.05$.

Principal component analyses (PCAs) based on NMR and PLFA results were performed to visualize the shift of C-chemistry and the composition of main microbial groups during straw decomposition in R statistical software v3.3.3 with the vegan package (Dixon 2003). Permutational multivariate analysis of variance (PERMANOVA) was further used to determine the significant differences in the C-chemistry and the composition of main microbial groups using the adonis function in the vegan package (Dixon 2003). Significant differences among the relative proportion of PLFAs between sampling times were detected using STAMP v2.1.1 (Parks et al. 2014). For the extended error bar plots, two-sided Welch's t test was used with Welch's inverted confidence interval method and Benjamin–Hochberg FDR multiple test correction ($P < 0.05$).

Multivariate regression tree (MRT) analysis was used to establish the relationship between residual C functional groups and the composition of main microbial groups in the mvpart (De'ath 2006), and the PLFAs explaining more than 5% difference for each split were identified by the MVPARTwrap (Ouellette and Legendre 2013) package in R. Prior to PCA and MRT analyses, the PLFAs ($\mu\text{g g}^{-1}$) data were $\log_{10}(x + 1)$ transformed.

Results

Biomass and C loss

Repeated ANOVA analysis showed that the biomass and C loss were not affected by soil texture during the 20-month period ($P > 0.05$; Table S1), whereas they were significantly influenced by the straw type, with the maize straw having a higher biomass and C loss than the wheat straw ($P < 0.05$; Table S1). The dynamics of the biomass and C loss of wheat and maize straws generally followed a similar pattern, increasing steadily during the first 10 months, followed by leveling off between 10 and 20 months in the three soils, except that the C loss of wheat straw in the sandy loam soil at 20 months was significantly higher than that at 10 months ($P < 0.05$; Fig. 1).

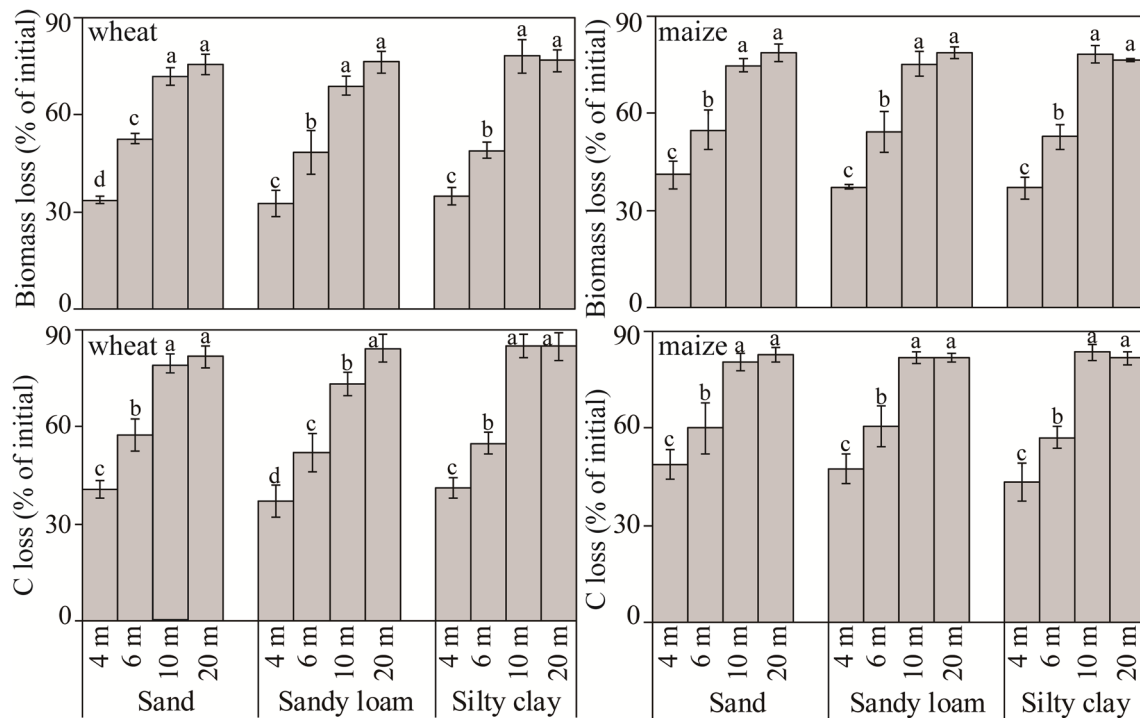


Fig. 1 Biomass and carbon (C) loss of wheat and maize straws after 4, 6, 10, and 20 months (m) of decomposition in three Calcaric Fluvisol soils differing for their texture (sand, sandy loam, and silty clay). Vertical bars

are standard errors of means ($n = 3$). Different letters above the columns indicate significant differences between decomposition times on the same soil texture ($P < 0.05$)

By considering values of the three soils, the biomass and C loss after 4, 6, 10, and 20 months averaged 34% and 40%, 50% and 55%, 73% and 79%, and 76% and 83%, respectively, for wheat straw and 38% and 47%, 54% and 59%, 76% and 82%, and 78% and 82%, respectively, for maize straw. The results further demonstrated that the C loss was more rapid than that of biomass at each decomposition time ($P < 0.05$).

Chemical composition

The ANOVA showed that three functional groups (alkyl C, aryl C, and O-aryl C) were significantly affected by the soil texture, while four functional groups (alkyl C, N-alkyl/methoxyl C, aryl C, and carboxyl/amide C) were affected by the straw type ($P < 0.05$; Table S2). Compared with the sand soil, the alkyl C content in the sandy loam and silty clay soils increased by an average of 2.8% and 9.2%, respectively, across the straw type and decomposition time, whereas the O-aryl and aryl C contents decreased by an average of 2.6–5.7% in sandy loam soil and 9.5–10.3% in silty clay soil (Table 2). Residual maize straw had lower alkyl C content (14.8% vs. 16.6%), but higher aryl (10.1% vs. 9.3%), N-alkyl/methoxyl (9.4% vs. 9.0%), and carboxyl/amide C (6.0% vs. 5.6%) contents than the residual wheat straw, across the soil texture and decomposition time (Table 2).

The temporal dynamics of various functional groups showed that significant decreases in di-O-alkyl (wheat 14.5% vs. 12.3%; maize 12.6% vs. 11.8%) and O-alkyl C

(wheat 62.0% vs. 53.3%; maize 57.2% vs. 51.9%) contents between 0 and 4 months were accompanied by the accumulation of alkyl (wheat 6.5% vs. 12.9%; maize 9.6% vs. 12.3%) and N-alkyl/methoxyl C (wheat 5.4% vs. 7.5%; maize 6.5% vs. 7.9%) ($P < 0.05$; Table 2). Between 4 and 6 months, the content of all the functional groups did not change significantly ($P > 0.05$; Table 2). Between 6 and 10 months, there was a substantial decrease in di-O-alkyl (wheat 11.9% vs. 9.2%; maize 11.9% vs. 9.5%) and O-alkyl C (wheat 51.7% vs. 37.7%; maize 51.6% vs. 38.0%) contents and an increase in alkyl (wheat 14.4% vs. 19.8%; maize 12.6% vs. 16.8%), aryl (wheat 7.2% vs. 10.9%; maize 8.0% vs. 11.8%), and carboxyl/amide C (wheat 3.7% vs. 6.1%; maize 3.7% vs. 6.6%) contents ($P < 0.05$; Table 2). Between 10 and 20 months, the major shift in the straw chemical structure was the continuous and significant decrease in di-O-alkyl (wheat 9.2% vs. 7.7%; maize 9.5% vs. 7.9%) and O-alkyl C (wheat 37.7% vs. 32.5%; maize 38.0% vs. 32.9%) contents and the accumulation of O-aryl (wheat 4.6% vs. 6.3%; maize 4.8% vs. 6.5%) and carboxyl/amide C contents (wheat 6.1% vs. 9.4%; maize 6.6% vs. 9.5%) ($P < 0.05$; Table 2).

Principal component analysis (PCA) of the functional groups contents showed that the PC1 and PC2 axes together accounted for more than 98% of the variation in the chemical composition of wheat (Fig. 2a) and maize (Fig. 2b) straws, with PC1 contributing to more than 93% in both straw types (Fig. 2). A similar temporal variation during the whole decomposition time, regardless of the soil texture, was observed for

Table 2 The percentages of total spectral area assigned to different functional groups and obtained by ^{13}C CP/MAS NMR for wheat and maize straws after 0, 4, 6, 10, and 20 months of decomposition in three Calcaric Fluvisol soils (sand, sandy loam, and silty clay)

Soil texture	Straw type	Time	220–190 ppm	190–165 ppm	165–142 ppm	142–110 ppm	110–93 ppm	93–60 ppm	60–45 ppm	45–0 ppm
			Ketone/aldehyde C	Carboxyl/amide C	O-aryl C	aryl C	di-O-alkyl C	O-alkyl C	N-alkyl/methoxyl C	Alkyl C
Sand	Wheat	0	0.87 c	2.64 c	2.45 c	6.03 c	14.46 a	62.00 a	5.45 d	6.49 c
		4	0.79 c	3.42 c	2.84 c	7.49 bc	12.12 b	52.42 b	7.73 c	13.18 b
		6	0.50 c	3.36 c	2.87 c	7.62 b	11.79 b	51.17 b	8.31 c	14.10 b
		10	2.22 b	6.40 b	5.08 b	11.83 a	9.48 c	38.00 c	9.65 b	17.34 a
		20	2.80 a	9.43 a	6.73 a	12.65 a	7.54 d	31.31 d	10.81 a	18.72 a
	Maize	0	0.85 c	4.37 c	2.51 c	6.41 c	12.65 a	57.24 a	6.53 d	9.61 c
		4	1.33 bc	4.99 bc	3.40 c	8.69 b	11.62 a	50.31 b	7.71 c	11.96 b
		6	0.96 c	3.56 c	2.87 c	8.08 b	12.19 a	52.15 b	8.51 b	11.82 b
		10	1.80 b	6.52 b	5.02 b	12.36 a	9.57 b	37.97 c	10.69 a	16.08 a
		20	2.72 a	9.74 a	6.68 a	13.14 a	7.75 c	31.73 d	11.10 a	17.14 a
Sandy loam	Wheat	0	0.87 b	2.64 c	2.45 c	6.03 b	14.46 a	62.00 a	5.45 c	6.49 c
		4	1.05 b	3.18 c	2.63 c	6.97 b	12.30 b	53.27 b	7.32 b	13.55 b
		6	1.22 b	4.13 bc	3.45 b	7.61 b	12.16 b	51.90 b	7.88 b	13.70 b
		10	1.29 b	4.74 b	4.04 b	12.04 a	9.76 c	39.49 c	10.10 a	17.51 a
		20	2.73 a	9.71 a	5.90 a	11.43 a	7.58 d	32.23 d	10.29 a	20.14 a
	Maize	0	0.85 c	4.37 c	2.51 d	6.41 c	12.65 a	57.24 a	6.53 d	9.61 c
		4	0.89 c	3.62 c	2.46 d	7.10 bc	12.12 b	53.90 b	7.91 c	12.24 b
		6	1.09 c	3.63 c	3.42 c	8.12 b	11.88 b	51.36 b	8.70 b	12.79 b
		10	2.06 b	6.88 b	5.12 b	12.26 a	9.38 c	36.80 c	10.73 a	16.78 a
		20	2.63 a	9.56 a	6.66 a	12.84 a	7.88 d	32.56 d	10.73 a	17.14 a
Silty clay	Wheat	0	0.87 c	2.64 c	2.45 c	6.03 c	14.46 a	62.00 a	5.45 c	6.49 d
		4	0.94 c	3.35 c	2.73 c	7.08 c	12.46 b	54.15 b	7.51 b	14.00 c
		6	1.08 c	3.56 c	2.81 bc	6.25 c	11.73 b	52.09 b	8.19 b	15.22 c
		10	1.69 b	6.28 b	3.68 b	9.92 b	8.37 c	35.70 c	9.67 a	24.70 a
		20	2.70 a	9.08 a	6.14 a	11.76 a	8.09 c	33.81 c	10.00 a	18.42 b
	Maize	0	0.85 c	4.37 c	2.51 d	6.41 b	12.65 a	57.24 a	6.53 c	9.61 c
		4	0.68 c	4.22 c	3.06 cd	7.93 b	11.80 b	51.51 b	8.00 b	12.62 b
		6	0.35 c	4.02 c	3.26 c	7.79 b	11.60 b	51.39 b	8.78 b	13.15 b
		10	1.84 b	6.34 b	4.28 b	10.84 a	9.48 c	39.18 c	10.36 a	17.68 a
		20	2.46 a	9.22 a	6.15 a	11.85 a	8.09 d	34.34 d	10.16 a	17.73 a

Data are means of three replicates. Lowercase letters refer to vertical (decomposition time) comparisons within each straw and soil at $P < 0.05$ NMR nuclear magnetic resonance

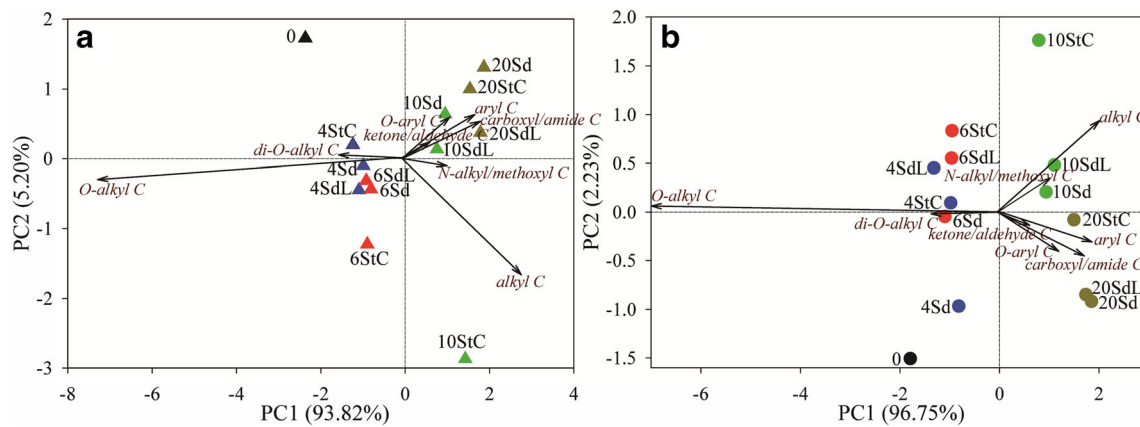


Fig. 2 Principal component analysis (PCA) of changes in chemical composition of wheat (**a**) and maize (**b**) straws based on the relative abundance of eight C functional groups over the 20-month decomposition period in three Calcaric Fluvisol soils differing for their

texture (sand, sandy loam, and silty clay). Different colors represent different decomposition times. The numbers of 0, 4, 6, 10, and 20 represent decomposition time (months). Sd, SdL, and StC stand for the soil texture of sand, sandy loam, and silty clay, respectively

both straw types. In addition, samples at 4 and 6 months had a similar chemical composition. The significant difference among 0, 4–6, 10, and 20 months was confirmed by PERMANOVA ($P < 0.05$; Table S3).

Composition of the main microbial groups

The PC1 and PC2 axes together accounted for 65.78% of the variation in the composition of the main microbial groups for wheat straw and 59.81% for maize straw (Fig. 3). A similar temporal variation in the composition of main microbial groups was observed for the both straw types during the whole decomposition time, regardless of the soil texture. The samples of both the straw types collected at 4 and 6 months or those collected at 10 and 20 months had similar compositions, when compared with those collected at 0 month. PERMANOVA further confirmed the significant difference among the three decomposition periods ($P < 0.001$; Table S4).

STAMP analysis was used to identify the specific PLFAs that significantly differed among the three decomposition periods (Fig. 4). Between 0 and 4–6 months, the significant changes ($> 3\%$) of main microbial groups associated to the wheat straw were represented by the increase in the fungal indicator 18:1 ω 9c (0 vs. 13.0%), in the G⁻ bacterial indicators 18:1 ω 7c (0 vs. 10.9%) and 16:1 ω 7c (2.7% vs. 8.0%), and a decrease in bacterial indicator 16:0 (61.5 vs. 24.0%) abundance ($P < 0.05$; Fig. 4a). The PLFAs of maize straw showed a significant increase in G⁻ bacterial indicators 18:1 ω 7c (0 vs. 11.2%) and 16:1 ω 7c (2.1% vs. 8.2%) and G⁺ bacterial indicators a15:0 (0.43 vs. 5.4%) and i15:0 (0.25 vs. 3.4%) and a decreased in fungal indicators 18:1 ω 9c (22.4% vs. 10.0%) and 18:2 ω 6,9c (21.8% vs. 17.2%) and the bacterial indicator 16:0 (41.8% vs. 21.8%) ($P < 0.05$; Fig. 4c). It must be noted that the fungal (18:1 ω 9c) abundance showed opposite changes in wheat compared to maize.

Between 4–6 months and 10–20 months, the proportions of the AMF indicator 16:1 ω 5c (wheat 1.1% vs. 13.3%; maize

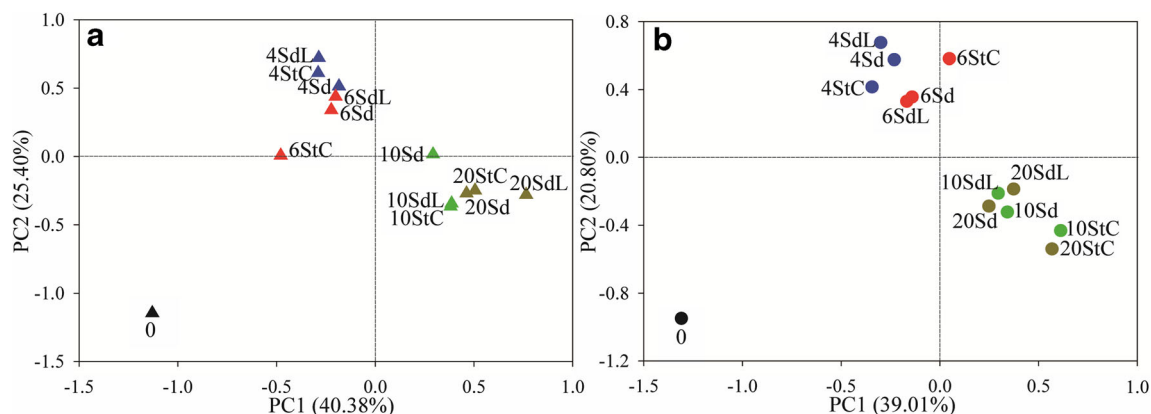


Fig. 3 Principal component analysis (PCA) of changes in the composition of main microbial groups of wheat (**a**) and maize (**b**) straws based on PLFA data over the 20-month decomposition period in three Calcaric Fluvisol soils differing for their texture (sand, sandy loam,

and silty clay). Different colors represent different decomposition times. The numbers of 0, 4, 6, 10, and 20 represent decomposition time (months). Sd, SdL, and StC stand for the soil texture of sand, sandy loam, and silty clay, respectively

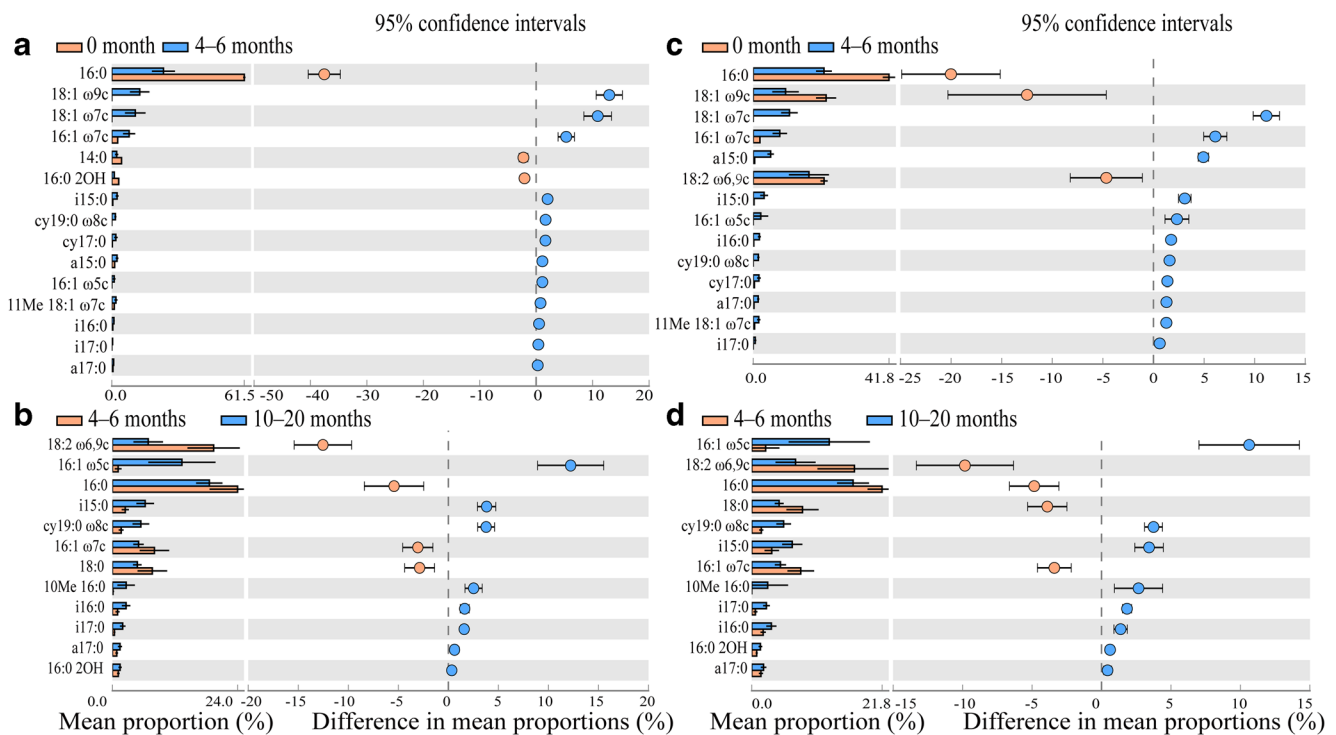


Fig. 4 Differences in mean relative proportions of various PLFAs that significantly differed between 0 and 4–6 months or between 4 and 6 months and 10–20 months for wheat (**a, b**) and maize (**c, d**) straws

2.3% vs. 13.0%), the G^+ bacterial indicator *i15:0* (wheat 2.3% vs. 6.3%; maize 3.4% vs. 6.8%), and the G^- bacterial indicator *cy19:0 ω 8c* (wheat 1.7% vs. 5.5%; maize 1.6% vs. 5.3%) significantly increased, whereas those of fungal indicator *18:2 ω 6,9c* (wheat 19.4% vs. 6.9%; maize 17.2% vs. 7.3%), the G^- bacterial indicator *16:1 ω 7c* (wheat 8.0% vs. 5.0%; maize 8.2% vs. 4.8%), and the bacterial indicators *16:0* (wheat 24.0% vs. 18.6%; maize 21.8% vs. 16.9%) and *18:0* (wheat 7.6% vs. 4.8%; maize 8.5% vs. 4.6%) significantly decreased in both wheat and maize straws ($P < 0.05$; Fig. 4b, d).

The total PLFA content and the ratio of F/B measured at 0 month were considerably higher in maize straw than those in wheat straw; however, the ratio of G^+/G^- was higher in wheat straw than that in maize straw (Table S5). During the first 4 months, the G^+/G^- ratio decreased and the F/B ratio increased in the wheat straw, while the G^+/G^- ratio increased and the F/B ratio decreased in the maize straw ($P < 0.001$; Table S5).

Relationships between the changes in the chemical structure of straw and in the composition of the main microbial groups

Multivariate regression tree (MRT) analysis was used to explore the relationships between the chemical structure of straw and the composition of main microbial groups during the whole 20-month decomposition period (Fig. 5). Figure 5 shows that the MRT explained 59.4% of the total variation in the composition of the main microbial groups in the wheat

straw, 42.8% of which was explained by the first split, which separated the samples into two main groups: the first group with samples at 0, 4, and 6 months, the second group with samples at 10 and 20 months. In particular, samples at 10 and 20 months were associated with higher alkyl C content ($\geq 17.0\%$). Changes in the abundances of AMF (*16:1 ω 5c*), G^+ (*i15:0*), G^- (*cy19:0 ω 8c*), and fungi (*18:2 ω 6,9c*) explained 86.4% of the variation in the composition of main microbial groups in the first split, with AMF explaining 51.6% of the variation. Further splitting of the samples at 0 month and those at 4 and 6 months depended on the N-alkyl/methoxyl C content. The samples at 4 and 6 months were associated with higher N-alkyl/methoxyl C content ($\geq 6.66\%$). Changes in the abundances of fungi (*18:1 ω 9c* and *18:2 ω 6,9c*), G^- (*18:1 ω 7c* and *16:1 ω 7c*), and bacteria (*16:0*) explained 93.9% of the variation in the composition of the main microbial groups in this split (Fig. 5a).

The MRT explained 50.3% of the total variation in the composition of main microbial groups in the maize straw, 39.5% of which was explained by the first split (Fig. 5b). The O-alkyl C separated the samples at 0, 4, and 6 months from those at 10 and 20 months in the first split and the lower content being associated with samples at 10 and 20 months ($< 44.2\%$). Changes in AMF (*16:1 ω 5c*), G^+ (*i15:0*), G^- (*cy19:0 ω 8c*), and fungal (*18:2 ω 6,9c*) abundances explained 83.5% of the variation in the composition of main microbial groups in the first split, 47.7% of which being explained by AMF. The di-O-alkyl C in the second split further separated

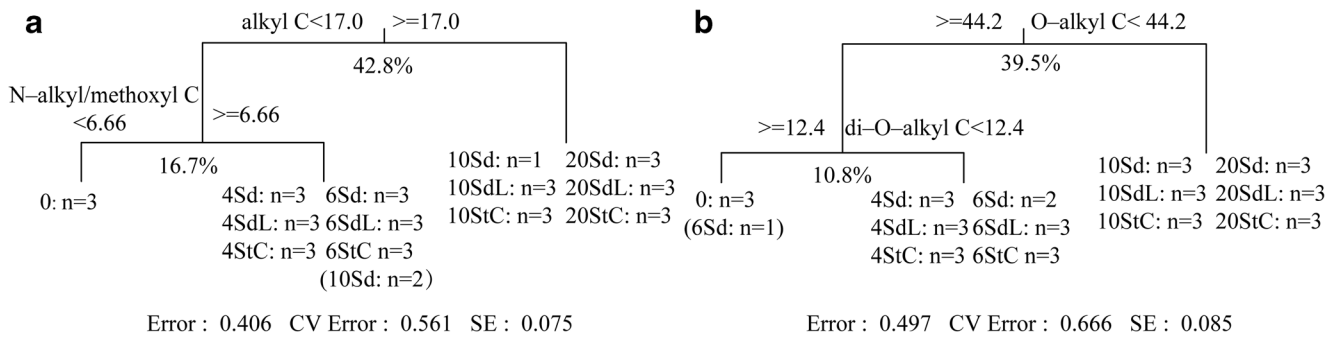


Fig. 5 Multivariate regression tree (MRT) analysis of the composition of main microbial groups based on PLFA data and chemical composition based on NMR data of wheat (a) and maize (b) straws over the 20-month decomposition period in three Calcaric Fluvisol soils differing for their texture (sand, sandy loam, and silty clay). Numbers under the crosses of each split indicate percentages of variation explained by the split. Specific

treatment regime and the numbers of samples included in the analysis are shown in each split. CV error represent cross-validation error; SE represent standard error of the tree. The numbers of 0, 4, 6, 10, and 20 represent decomposition time (months). Sd, SdL, and StC stand for the soil texture of sand, sandy loam, and silty clay, respectively

the samples at 0 month from those at 4 and 6 months, explaining 10.8% of the variance. Samples at 4 and 6 months were associated with lower di-O-alkyl C content (< 12.4%). Changes in the fungal (18:1 ω 9c and 18:2 ω 6,9c), G[−] (18:1 ω 7c and 16:1 ω 7c), G⁺ (a15:0), and bacterial (16:0) abundances explained 90.0% of the variation in the composition of main microbial groups in this split.

Pearson's correlation analysis of the chemical and microbial groups showed significant change between 0 and 4 months or between 6 and 10 months (Table 3). The functional groups were selected according to the data of Fig. 2 and Table 2. We

selected PLFA biomarkers that explained most of the variation in the composition of the main microbial groups (Fig. 5) and significantly changed between sampling times (Fig. 4).

The correlation analyses showed that between 0 and 4 months, the fungal (18:1 ω 9c) and G[−] (18:1 ω 7c and 16:1 ω 7c) abundances of the wheat straw showed a positive association with alkyl and N-alkyl/methoxyl C contents and a negative association with di-O-alkyl and O-alkyl C contents ($P < 0.05$; Table 3). In the case of maize straw, the alkyl and N-alkyl/methoxyl C contents showed a positive correlation with the G⁺ (a15:0) and G[−] (18:1 ω 7c and 16:1 ω 7c) abundances

Table 3 Correlation coefficients between the contents of functional groups and the abundances of PLFAs that both significantly changed between 0 and 4 months or between 6 and 10 months

Decomposition period	Straw	PLFA	Alkyl C	N-alkyl/methoxyl C	O-alkyl C	Di-O-alkyl C	Aryl C	Carboxyl/amide C
0 to 4 months	Wheat	18:1 ω 9c	0.827**	0.728**	−0.814**	−0.863**	na	na
		18:1 ω 7c	0.672*	0.693*	−0.749**	−0.780**	na	na
		16:1 ω 7c	0.814**	0.756**	−0.835**	−0.877**	na	na
		16:00	0.579*	ns	ns	ns	na	na
	Maize	18:1 ω 9c	−0.702*	−0.732**	0.883**	0.795**	na	na
		18:1 ω 7c	0.813**	0.867**	−0.822**	−0.857**	na	na
		16:1 ω 7c	0.778**	0.837**	−0.827**	−0.797**	na	na
		16:00	ns	ns	ns	ns	na	na
		18:2 ω 6,9c	ns	0.606*	ns	ns	na	na
		a15:0	0.643*	0.712**	−0.854**	−0.776**	na	na
6 to 10 months	Wheat	16:1 ω 5c	0.656*	na	−0.765**	−0.771**	0.609**	0.678**
		i15:0	ns	na	−0.491*	ns	0.473*	ns
		cy19:0 ω 8c	0.599**	na	−0.772**	−0.731**	0.665**	0.626**
		18:2 ω 6,9c	−0.648*	na	0.481*	0.595**	ns	ns
	Maize	16:1 ω 5c	0.568*	na	−0.608**	−0.625**	0.547*	0.621*
		i15:0	0.541*	na	ns	−0.495*	ns	ns
		cy19:0 ω 8c	0.772**	na	−0.763**	−0.773**	0.684**	0.715**
		18:2 ω 6,9c	−0.453	na	0.469*	0.437	ns	ns

PLFA phospholipid fatty acids, ns non-significant at $P = 0.05$,

* $P < 0.05$; ** $P < 0.01$ significance

and a negative correlation with the fungal (18:1 ω 9c) abundance, while the di-O-alkyl and O-alkyl C contents showed a negative correlation with the G⁺ (a15:0) and G⁻ (18:1 ω 7c and 16:1 ω 7c) abundances and a positive correlation with the fungal (18:1 ω 9c) abundance ($P < 0.05$). Between 6 and 10 months, the di-O-alkyl and O-alkyl C contents in both wheat and maize straws were negatively correlated with the AMF (16:1 ω 5c) and G⁻ (cy19:0 ω 8c) abundances, whereas the alkyl, aryl, and carboxyl/amide C contents in both straw types were positively correlated with the abundance of the two above-mentioned PLFA biomarkers ($P < 0.05$). In addition, the di-O-alkyl and O-alkyl C contents were positively correlated, and the alkyl C content was negatively correlated with the fungal (18:2 ω 6,9c) abundance in both wheat and maize straws (Table 3).

Discussion

The biomass and C loss patterns of both straws in soils differing for their texture

The rapid biomass and C loss (75–79% of biomass and 81–85% of C were lost) of both wheat and maize straws in the first 10 months were followed by a leveled off pattern, regardless of the soil texture (Fig. 1). The C loss was faster than the biomass ($P < 0.05$), probably due to the slow release of N, P, S, and Ca from straw during decomposition (Ribeiro et al. 2002). It is established that the decomposition of most organic materials consists of two distinct phases: the initial rapid loss of easily decomposable compounds, during which 60–80% of the biomass and C are lost, followed by the slower loss due to the degradation of recalcitrant compounds (Wang et al. 2004; Powell et al. 2009; Preston et al. 2009; Grandy et al. 2013). However, the time period of the rapid degradation usually varies considerably depending on the material types and the environmental conditions. For example, Powell et al. (2009) showed that the rapid decomposition of soybean and maize straws occurred in the first 5 months after they were buried in the field, whereas Preston et al. (2009) found that approximately 80% of the mass of the 10 different foliar litters were lost during the first 5 years of decomposition in cold regions.

The maize straw decomposed faster than wheat straw over the 20-month period (Fig. 1), which contradicts what reported by Wang et al. (2012), probably due to the different environmental conditions. In addition, the soil texture had little effect on the biomass and C loss of both straws (Table S1). This result is consistent with what reported by Scott et al. (1996), and it may depend on the limited contact between clay minerals and organic materials (Baumann et al. 2009). Besides, litterbags exclude the influence of soil fauna, which have a major role in straw degradation and also can form microhabitat that slightly differs from the natural conditions (Baumann

et al. 2009; Wickings et al. 2012). However, the litterbag method is still a popular technique to explore the mechanisms of straw decomposition in soil (Marschner et al. 2011; Baumann et al. 2013; Bonanomi et al. 2019).

Changes in the chemical structure of both straws in soils differing for their texture

Significant losses of di-O-alkyl and O-alkyl C were observed for both straw types during the 0–4-month period (Fig. 2; Table 2), confirming what already reported (Baldock et al. 1997; Mathers et al. 2007; Baumann et al. 2013), since these functional groups are associated with carbohydrates (Mathers et al. 2007), which are labile compounds easily degraded by microorganisms (Mathers et al. 2007; Yin et al. 2014). Additionally, the accumulation of alkyl and N-alkyl/methoxyl C occurred during this period (Fig. 2; Table 2). Alkyl C is associated with alkyl chain ($-\text{CH}_2-$) of waxes, cutins, suberins, or lipids (Baumann et al. 2009); hence, the accumulation of recalcitrant alkyl C may be due to the selective preservation of these aliphatic biomacromolecules, whose degradation requires high energy and specific enzymes (Winkler et al. 2005; Baumann et al. 2009). As N-alkyl C is associated with proteins and peptides, and methoxyl C is associated with recalcitrant lignin (Li et al. 2015), it can be inferred that the rapid accumulation of N-alkyl/methoxyl C could probably be due to the preservation of methoxyl C and formation of new N-alkyl compounds, such as bacterial peptidoglycan and fungal chitin, in cell wall (De Marco et al. 2012; Li et al. 2015).

The chemical composition of residual straw was similar at 4 and 6 months (Fig. 2; Table 2), despite the steady loss of biomass and C during this period (Fig. 1), suggesting a similar degradation of the various straw components. This confirms what were reported by Chabbi and Rumpel (2004) and Baumann et al. (2013).

The continuous decrease in di-O-alkyl and O-alkyl C contents observed during the 6–10- and 10–20-month periods (Fig. 2; Table 2) may be due to the role of these components as active C pool and activation energy resources for microorganisms to degrade recalcitrant structure under limited nutrient conditions (Xu et al. 2017). Meanwhile, the significant increase in alkyl C content during the 6–10-month period may be due not only to the recalcitrant components of straw but also to the transformation of labile C into structural microbial C, such as nonpolar alkyl C and storage lipids (Lundberg et al. 2001). The aryl and O-aryl C represent the aromatic and phenolic C of lignin, respectively (Carvalho et al. 2009). Hilscher and Knicker (2011) suggested that the partial oxidation of the aryl structure occurred by two processes: enzymatic hydroxylation of aryl C to form O-aryl C and oxygenation and cleavage of O-aryl ring to produce carboxyl C. The O-aryl C is easily degraded compared with aryl C (Geng and Li 2002). The observed significant enrichment of aryl C during the 6–

10-month period and the enrichment of O-aryl C during the 10–20-month period (Table 2) may be attributed to the type of the dominant process. During the 6–10-month period, the O-aryl C decay process probably dominated over the aryl C decay process, and during the 10–20-month period, the aryl C decay likely became the dominant process.

Changes in the composition of main microbial groups of both straws in soils differing for their texture

Between 0 and 4–6 months, divergence in the composition of the main microbial groups in wheat straw was due to the enrichment of G^- bacteria (18:1 ω 7c and 16:1 ω 7c) and fungi (18:1 ω 9c) (Figs. 3a and 4a), whereas it was due to the enrichment of G^- bacteria (18:1 ω 7c and 16:1 ω 7c) and G^+ bacteria (a15:0 and i15:0) and the depletion of fungi (18:1 ω 9c and 18:2 ω 6,9c) in the maize straw (Figs. 3b and 4c). Li et al. (2018) revealed that G^- bacteria (18:1 ω 7c and 16:1 ω 7c) actively participated in degrading maize straw. Moore-Kucera and Dick (2008) showed that fungi (18:1 ω 9c) played an important role in decomposing the needles of Douglas-fir during the first 5 months of decomposition. Gram-negative bacteria are fast-growing r-strategists that grow quickly using easily degradable compounds (Derrien et al. 2014); fungi are considered key agents of litter decay (Berg et al. 2015). In addition, the involvement of G^+ bacteria in maize straw decomposition was not a surprise, as Bray et al. (2012) reported that many of the known cellulolytic bacteria are G^+ .

It is noted that between 0 and 4–6 months, the abundance of fungi (18:1 ω 9c) decreased in the maize straw while it increased in the wheat straw (Fig. 4a, c), and this may depend on the different initial quality of both straws. The wheat straw had a higher content of easily decomposable compounds than did the maize straw (Table 2), which indicated that the content of C sources may be high enough to support the growth of fungi and G^- bacteria in the wheat straw, while in the maize straw, the fungal growth was likely suppressed by the bacterial growth due to the intense competition for C sources between them (Romani et al. 2006; Marschner et al. 2011). This hypothesis can be partly supported by the fact that the G^+/G^- ratio increased and the F/B ratio decreased between 0 and 4–6 months in the maize straw, but the opposite trend occurred in the wheat straw (Table S5). The increase in the G^+/G^- ratio reflected a progressive shift from copiotrophic to oligotrophic conditions when the microbial community responded to the changed C availability (Yao et al. 2000), and the F/B ratio depends on the environmental conditions such as the available C content (Prosser et al. 2007).

Between 4–6 and 10–20 months, the significant difference in the composition of main microbial groups in both wheat and maize straws was due to the increases in AMF (16:1 ω 5c), G^+ (i15:0), and G^- (cy19:0 ω 8c) and the decrease in the fungal (18:2 ω 6,9c) proportions (Figs. 3 and 4b, d). The AMF can

promote litter decomposition by stimulating the activity of hyphosphere bacteria (Hodge et al. 2001). Li et al. (2018) used ^{13}C -labeled maize straw and found that AMF (16:1 ω 5c) were effectively involved in degrading maize straw. Our results showed an increase in G^- bacteria and a decrease in the fungal proportion in the later period, confirming what reported by Moore-Kucera and Dick (2008), who showed that during the period between 9 and 22 months, the assimilation of the residue-derived C by fungi decreased while that by G^- bacteria increased. The G^+ bacteria are considered slow-growing species, and an increase in their abundance during the later stage of decay has been reported by Bray et al. (2012). Swift et al. (1979) demonstrated that bacteria were replaced by fungi-dominated microbial communities during litter decay, with changes in the composition of both the microbial groups. Our results suggest that the succession of bacteria and fungi during the decomposition period depended on the straw type.

The similar composition of the main microbial groups between 4–6 and 10–20 months was observed for both straw types (Figs. 3 and 5). Bray et al. (2012) reported that the similar microbial community composition in forest residues after 1- and 2-month decomposition was due to the presence of easily degradable compounds, while García-Palacios et al. (2016) attributed the similar microbial community composition in litter mixtures after 7- and 11-month decomposition to the similar chemical characteristics of residues at this stage. Accordingly, the similar composition of main microbial groups between 4 and 6 months could probably be the result of comparable chemical structures of wheat and maize straws during this stage (Table 2; Fig. 2); nevertheless, the reasons for the similar composition of main microbial groups between 10 and 20 months are unknown.

Relationships between the changes in the chemical structure of straw and the shifts in the composition of main microbial groups at different decomposition periods

The composition of the main microbial groups during the straw decomposition was generally determined by alkyl C and N-alkyl/methoxyl C contents of wheat straw and by O-alkyl C and di-O-alkyl C contents of maize straw (Fig. 5). Baumann et al. (2009) inferred that N-alkyl/methoxyl C, which represents the easily available N in proteins or nucleotides compounds, influenced the succession of microbial community during straw decomposition. Our results indicate that the change in recalcitrant aliphatic compounds and easily available N played a crucial role in microbial succession in the decomposing wheat straw, whereas the carbohydrate content strongly influenced the composition of main microbial groups in the decomposing maize straw.

Between 0 and 4 months, both fungal (18:1 ω 9c) and G^- (16:1 ω 7c and 18:1 ω 7c) abundances showed strong negative

associations with di-O-alkyl and O-alkyl C contents of wheat straw (Table 3). The di-O-alkyl and O-alkyl C contents, which represent the active C pool of straw, can be preferentially utilized by both fungal and bacterial species to gain energy during decomposition (Baldock et al. 1997). The strong negative associations between G^- bacterial abundance and di-O-alkyl and O-alkyl C contents confirmed the results reported by Xu et al. (2017).

Unlike wheat straw, a negative association between G^+ abundance and di-O-alkyl and O-alkyl C contents and a positive association between fungal (18:1 ω 9c) abundance and di-O-alkyl and O-alkyl C contents between 0 and 4 months were observed for the maize straw (Table 3). The G^+ bacteria are involved in the decomposition of available C compounds, which is accompanied by an increase in the recalcitrant alkyl C content (Baumann et al. 2011). Accordingly, a positive association between G^+ bacteria and alkyl C (Table 3) was found in this study. Decomposer fungi are divided into “sugar fungi” and cellulytic and ligninolytic fungi, with the former utilizing carbohydrate substrates and the latter decomposing stable cellulose and lignin compounds (Bonanomi et al. 2019). The fungal hyphae are capable of penetrating into recalcitrant materials and degrading these compounds into decomposable molecules (Xu et al. 2017). Accordingly, a positive association was noted between fungal abundance and di-O-alkyl and O-alkyl C contents and a negative association was detected between fungal abundance and alkyl C content of the maize straw (Table 3). Our results suggest that in the wheat straw, the “sugar fungi” mainly participated in the degradation of readily decomposable components, while in the maize straw, the cellulytic and ligninolytic fungi participated in the breakdown of refractory components. Between 4 and 6 months, the similar composition of the chemical structure of straw and main microbial groups suggests the coexistence of microbial species, which degraded various straw components simultaneously.

Between 6 and 10 months, the relationships between the C functional groups and the specific microbial groups of the wheat and maize straws were similar (Table 3). The negative associations between AMF (16:1 ω 5c) and di-O-alkyl and O-alkyl C suggest that the AMF species might have promoted straw decomposition in the later decomposition period, and this is confirmed by the data that AMF mainly explained the variation in the composition of main microbial groups between samples collected at 0, 4, and 6 months and those collected at 10 and 20 months (Fig. 5). Li et al. (2018) found that the AMF (16:1 ω 5c) assimilated maize-derived C, while Pei et al. (2017) found that the AMF (16:1 ω 5c) abundance had a positive relationship with phenol oxidase and peroxidase activities, which were involved in phenolic lignin degradation. These findings may explain the positive association between AMF (16:1 ω 5c) and aryl and carboxyl/amide C (Table 3). The abundance of the fungal indicator 18:2 ω 6,9c was

negatively correlated with alkyl C content and positively correlated with di-O-alkyl and O-alkyl C contents during 6–10-month period, which suggests that fungal species are involved in the degradation of recalcitrant alkyl C during this stage.

Between 10 and 20 months, the changed chemical structure of both residual straws was characterized by the increased contents of di-O-alkyl and O-alkyl C and the decreased contents of O-aryl C and carboxyl/amide (Fig. 2; Table 2), while the composition of main microbial groups being similar between 10 and 20 months (Fig. 3). This result suggests that the transformation of different functional groups between 10 and 20 months may be attributed to changes microbial functions and not in the composition of main microbial groups. Wallenstein et al. (2010) reported that the similar microbial communities could exhibit a diverse physiology and different degradation pathways.

Conclusions

Our decomposition experiment based on the use of the litterbag method revealed that soil texture was not an important factor. Generally, the alkyl C and N-alkyl/methoxyl C contents were the most influential factors in determining the composition of the main microbial groups during wheat straw decomposition, while during the maize straw decomposition, the O-alkyl C and di-O-alkyl C contents were the best predictors of the composition of the main microbial groups. Relationships between the changed chemical structure and the shifts in the composition of main microbial groups differed in the wheat straw and maize straws during the first 4 months, mainly due to the decrease in di-O-alkyl and O-alkyl C contents and the increase in alkyl and N-alkyl/methoxyl C contents relating to the enrichment of fungi (18:1 ω 9c) in wheat straw and to a depletion of fungi (18:1 ω 9c) in maize straw. During the 6–10-month period, the relationships between the changed chemical structure and the shifts in the composition of main microbial groups became similar for both straw types, namely, the decrease of the di-O-alkyl and O-alkyl C and the increase of the alkyl, aryl, and carboxyl/amide C contents were mainly associated with the enrichment of AMF (16:1 ω 5c). These results confirmed our hypothesis that during crop straw decomposition, the relationships between the chemical structure and the composition of main microbial groups of the residual straw varied with the straw type and the decomposition period. Our results contribute to the knowledge of the straw degradation pathway under field conditions and emphasize the importance of straw type and decomposition period as determinants of the chemical and microbial changes that occur during the straw degradation.

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