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Lasting effect of repeated application of organic waste products on microbial communities in arable soils

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ABSTRACT

Using organic waste products (OWP) in agriculture makes it possible to increase productivity with less use of mineral fertilizers. However, the lasting effect on soil microbial communities of an OWP application repeated over several years needs further investigation. In the present study, soils were sampled from two long-term field experiments: QualiAgro and Colmar (France), where different types of OWP characterized by more or less stable organic matter had been applied for more than 10 years, and were compared to a control treatment. At QualiAgro, the carbon inputs due to OWP application were greater (~4 t C ha^{-1} every two years) than at Colmar (~1.7 t C ha^{-1} every two years). On both sites, soil samples were taken more than six months after the last OWP input. At QualiAgro, soil organic carbon, N and P_2O_5 concentrations, pH, and CEC were increased by repeated OWP inputs, as compared to the control. Soil microbial community parameters were also lastingly affected by OWP application. A 50% increase in microbial biomass was observed with OWP with the most stable organic matter contents. The prokaryotic community structure was influenced: directly by the OWP applied, and indirectly by soil properties changes. Soil pH appeared as a major driver for structure of the soil prokaryotic community. Fungal community structure was only directly influenced by the OWP applied. Contrastingly, at Colmar, OWP application had no impact on soil chemical characteristics or microbial communities' parameters. This was probably due to the smaller amount of OWP applied than at QualiAgro, and/or a longer delay between the OWP application and soil sampling. Altogether, our results show that, depending on its type, the applied OWP could produce a lasting increase in soil microbial biomass and shape microbial community structure.

1. Introduction

Intensive agricultural practices contribute to a decrease in soil organic matter content, with negative consequences on soil fertility (Clapp et al., 1986; Tate, 1987). One way to reverse this degradation in soil fertility is to increase soil organic matter content by applying organic amendments such as manures, composts, or crop residues (Hutchinson et al., 2007; Peltre et al., 2012). Which, at the same time could contribute to mitigate greenhouse gas emissions (Lal, 2004) and thus indirectly climate change. Nevertheless, the effectiveness of these measures depends upon both the soil characteristics and the current SOC content (Merante et al., 2017).

Among the different organic inputs, organic waste products (OWP) resulting from human activities (i.e. sewage sludge, municipal solid waste composts, farmyard manure) are being increasingly used because they facilitate the recycling of nutrients and improve soil fertility. Indeed, organic fertilization is known to enhance (i) soil physical fertility by improving soil porosity, aggregation and structure stability, bulk density and water holding capacity (Abiven et al., 2009; Annabi et al., 2011; Eden et al., 2017) and (ii) chemical fertility through pH regulation, as well as increased CEC and availability of nutrients (Diacono and Montemurro, 2010; Chalhoub et al., 2013). These modifications of soil physico-chemical properties consequently impact the biological components of soil, especially the soil microbial communities. In the field, many studies focused on the impact of a single application of OWP, and highlighted an increase in microbial biomass and activity, and a change of soil microbial community structure (García-Gil et al., 2004; Calbrix et al., 2007; Bastida et al., 2008; Bastida et al., 2013; Lazcano et al., 2013; Federici et al., 2017). Monitoring the dynamics of these changes revealed that OWP (~5 Mg ha^{-1} applied)

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initially induced strong changes in bacterial functional and genetic structures during the first 3 months after amendment, followed by a period of resilience leading after 6 months to similar communities in both amended and control plots (Calbrix et al., 2007). Previous research thus suggests that a single OWP application has a transient impact on the abundance and diversity of soil microbial communities. This transient effect of a single dose of organic amendments in soil microbial community seemed however dependent to the quantity applied, since a persistent effect has already been observed with 195 Mg ha^{-1} of OWP applied (Bastida et al., 2013).

Repeated fertilization over several years is a commonly used practice under field conditions to maintain soil fertility and thus crop yields. In comparison to a single OWP application, it was also observed that repeated fertilization had more persistent impact on soil characteristics (Rousk et al., 2011; Körschens et al., 2013), plant growth (Clark et al., 2007), and microbial diversity and activity (Hartmann et al., 2015; Francioli et al., 2016). All studies focusing on the impact of a repeated organic fertilization on soil microbial communities demonstrated an increase in soil microbial biomass (Crecchio et al., 2004; Zhong et al., 2010; Poulsen et al., 2013a; Poulsen et al., 2013b; Francioli et al., 2016). However, the response of other soil microbial community parameters (diversity, composition (i.e. inventory of present species), structure (i.e. number and relative abundance of present species in the community)) seemed to depend on the time between the OWP application and soil sampling, and the duration of the application (Crecchio et al., 2004; Zhong et al., 2010; Poulsen et al., 2013a; Francioli et al., 2016). The short-term response of these parameters to a repeated OWP application (until 5 months after the application) was similar whatever the duration of the application (8–70 years), with an increase of soil microbial diversity, and a change of microbial community composition (Parham et al., 2003; Ros et al., 2006; Chen et al., 2016). The lasting effect of OWP application on these parameters (from six months after the application) seems to depend on the duration of the application, as no lasting change of soil bacterial community structure and composition was observed after 6 years of application (Crecchio et al., 2004; Poulsen et al., 2013a), whereas an increase of soil bacterial and fungal communities diversity and a stimulation of some microbial groups (*Firmicutes*, *Proteobatcreia*, and *Zygomycota*) were observed after more than 20 years (Zhong et al., 2010; Francioli et al., 2016). Six years of OWP application were probably not sufficient to result in a lasting modification of soil physico-chemical properties and indirectly lasting change soil microbial community. Further studies are needed to assess the minimum number of repeated applications required to induce a lasting effect of OWP on the diversity and composition of soil microbial communities.

Other parameters, such the quantity and type of materials applied, might influence the impact of OWP on soil microbial communities (Diacono and Montemurro, 2010). Reports in the literature about the effect of different OWP on soil microbial communities are rare. Only Poulsen et al. (2013a,b) assessed the lasting effect of different types of OWP (human urine, compost, cattle manure and sewage sludge), but this study was restricted to soil bacterial communities. According to Zhong et al. (2010) and Francioli et al. (2016), the aforementioned effects of OWP application on soil microbial communities in the long term are caused indirectly by OWP-induced changes of soil properties. Soil bacterial and fungal communities may therefore also respond differently to different types of applied organic amendments since Obriot et al. (2016) observed that soil chemical properties were differently affected by a repeated application of these products. To our knowledge, the effect of different types of OWP on soil bacterial and fungal communities has never been assessed simultaneously.

This was therefore the purpose of the present study involving two long-term field experiments (QualiAgro and Colmar). We hypothesized that the lasting effect of OWP inputs might (i) be related to the type of OWP, more precisely to the degradability, and (ii) depend on soil parameters. We expected that after more than 10 years of OWP repeated application, the soil's physico-chemical status would be lastingly modified, resulting in a lasting change in the diversity and abundance of the soil microbial communities. Each field experiment involved different types of organic waste products and pedo-climatic conditions (especially soil type and climate) and had received OWP applications for more than 10 years. The responses of prokaryotic and fungal communities to OWP were assessed by a high throughput sequencing approach targeting 16S and 18S ribosomal genes. All soil samples were collected more than six months after the OWP application.

2. Material and methods

2.1. Experimental sites, soil sampling strategy and soil chemical analysis

The experiment was carried out on two field stations (QualiAgro and Colmar) belonging to the SOERE-PRO-network (https://www6.inra.fr/qualiagro_eng/Nos-partenaires/The-SOERE-PRO-network).

The QualiAgro experiment is located at Feucherolles in northwestern France (35 km west of Paris; 48°52′ N, 1°57′ E, alt 150 m). The soil is a Luvisol (WRB, 2015) containing 16% clay, 78% silt, and 6% sand on average in its tilled layer. The climate is oceanic with a mean rainfall of 594 mm year^{-1} and a mean annual temperature of 10.8 °C. The experimental field site has been cropped with a wheat-maize rotation since the beginning of the experiment. The wheat (*Triticum aestivum*) crop residues have been exported, whereas the maize (*Zea mays*) residues have been returned to the soil. Four different organic amendments have been applied: (1) a municipal solid waste compost (MSW) made from residual municipal wastes after the selective collection of dry and clean packaging; (2) a biowaste compost (BIO) made from the selectively collected fermentable fractions of municipal wastes co-composted with green wastes; (3) a compost resulting from the co-composting of sewage sludge, green wastes and wood chips (GWS); and (4) a farmyard manure (FYM) obtained from a dairy farm. These four organic treatments were compared to a control treatment that has not received any organic input (CON). Each treatment was replicated three times, and the experimental plots were arranged in a randomized complete block design. Each 10 m × 45 m plot was separated by 6-m-wide cultivated bands and the blocks by 25-m-wide cultivated strips. Additionally, all plots received a low level of mineral nitrogen (60 kg N ha^{-1}) for wheat and maize, in spring. Since 1998, the OWP have been applied at a rate of ~4 Mg C ha^{-1} every two years on the wheat stubble in September, after harvesting.

Colmar is located in northeastern France (380 km east of Paris; 48°08′ N, 7°36′ E, alt 175 m). The soil is a Calcosol (WRB, 2015) containing 21% clay, 70% silt, and 9% sand on average in its tilled layer. The climate is continental with a mean rainfall of 567 mm year^{-1} and a mean annual temperature of 10.5 °C. The experimental field site has been cropped with a maize (*Zea mays*) – winter wheat (*Triticum aestivum*) – beet (*Beta vulgaris*) – barley (*Hordeum vulgare*) rotation, in which all crop residues were returned. The experiment has a randomized complete block design with 3 replicates comparing 6 organic fertilizer treatments: BIO, GWS, FYM, FYMc (composted farmyard manure), SLU (non-composted sewage sludge) and CON. As for QualiAgro, CON was considered as the control treatment. Each 9 m × 10 m plot was separated by 6 m wide cultivated bands and the blocks by 10 m wide cultivated strips. In contrast to QualiAgro, no mineral nitrogen has been applied to the plots. Since 2001, the OWP have been applied at a rate of ~1.7 Mg C ha^{-1} every two years before maize or sugar beet. The last OWP application was in December 2010.

Analyses of pH, organic C and total N were performed to characterize each OWP. Before analysis, the organic amendments were dried and ground to 1 mm. The total N and organic C contents were measured by elemental analysis (NA 1500, Fison Instrument, San Carlos, CA, USA) after additional grinding to 200 µm (Retsch SM 2000, Haan, Germany). The index of residual organic carbon (I_{ROC}) that

Table 1
Characteristics of organic waste products applied in QualiAgro and Colmar between 1998 and 2011, and 2001 and 2010 respectively.

Treatment	Dry matter (DM) %	Applied quantity t DM ha^{-1}	Organic carbon g kg^{-1} DM	I_{ROC} % Org C	Total N g kg^{-1} DM	C:N	pH (water)
QualiAgro							
BIO	70.1a	19.1a	208b	75a	17.4b	12.1b	8.1ab
FYM	39.6b	13.2a	320a	67ab	21.9ab	14.7ab	9.1a
GWS	63.3a	16.4a	265ab	77a	23.5a	11.4b	7.5b
MSW	67.8a	12.0a	308a	49b	17.6b	17.8a	7.5b
Effect of organic waste product†	*	**	***	**	***	**	*
Colmar							
BIO	57.7a	8.4a	238c	73a	19.4c	12.6a	8.5b
FYM	19.7b	7.1ab	394a	60b	26.7b	15.2a	9.5a
FYMc	19.4b	6.1b	354ab	69ab	25.9b	14.0a	9.4ab
GWS	52.9a	7.1ab	303b	72ab	25.1b	12.1a	7.6c
SLU	17.8b	2.7c	368a	44c	59.7a	6.3b	7.2c
Effect of organic waste product	***	**	***	***	***	***	***

* Significant at the 0.05 probability level.
** Significant at the 0.01 probability level.
*** Significant at the 0.001 probability level.
† Values with the same lower case letters in a column and within a research site are not significantly different at $P < 0.05$.

represents the proportion of organic matter potentially incorporated into soil organic matter after OWP application (Lashermes et al., 2009) was also determined. The mean OWP characteristics measured between 1998 and 2011 for QualiAgro, and between 2001 and 2010 for Colmar are given in Table 1.

Soils samples were collected in March 2012 on bulk soils after the 7th OWP application at QualiAgro and the 6th application at Colmar. In each plot, 5 soil cores (Ø7 cm) were randomly taken at 0–25 cm depth, then mixed and homogenized by passing them through a 4 mm sieve to remove above-ground plant debris, roots and stones. Fifteen soils at QualiAgro (5 treatments × 3 replicates) and eighteen soils at Colmar (6 treatments × 3 replicates) have been sampled. A portion of each soil was dried for physico-chemical analysis. Particle size distribution, pH, soil organic matter, soil organic carbon, soil total nitrogen (N), soil C/N ratio, Olsen P and Cation Exchange Capacity (CEC), were determined by the Soil Analysis Laboratory at INRA ARRAS, France (http://www.lille.inra.fr/las). Soil physico-chemical data collected from the same sampled plots, before the first OWP application (1998 for QualiAgro and 2001 for Colmar), are also presented (Tables 2 and 3). The rest of the sampled, sieved soil was lyophilized and stored at −40 °C until used for molecular analyses based on soil DNA extraction.

2.2. DNA extraction and purification

Microbial DNA was extracted from 1 g (dry weight) of soil using a single procedure standardized by the GenoSol platform (INRA, Dijon, France, www.dijon.inra.fr/plateforme_genosol) (Terrat et al., 2012). Since a highly positive linear relationship has been shown between soil DNA recovery and C-biomass measurement (Ranjard et al., 2003), DNA concentrations of crude extracts were determined by electrophoresis in 1% agarose gel stained with ethidium bromide using a calf thymus DNA standard curve, and used as estimates of microbial biomass (Dequiedt et al., 2011). After quantification, nucleic acids were separated from the residual impurities, particularly humic substances, by centrifuging through two types of minicolumn. Aliquots (100 µL) of crude DNA extract were first loaded onto polyvinyl polypyrrolidone minicolumns (BIORAD, Marne-la-Coquette, France) and centrifuged at 1000 × *g* for 4 min at 10 °C. The eluates were then purified using the Geneclean turbo kit (Mp Biomedicals, Illkirch, France) (Ranjard et al., 2003). Purified DNA concentrations were finally measured using the Quantifluor (Promega, Lyon, France) staining kit, according to the manufacturer's instructions.

Table 2
Soil physico-chemical parameters from QualiAgro, according to organic waste products applied and sampling time.†

Treatment	Clay	Silt	Sand	Organic carbon***	N***	P_2O_5 (Olsen)***	C:N***	pH (water)***	CEC***
	g kg^{-1}			g kg^{-1} DM					cmol + kg^{-1} DM
BIO									
1998	15.83	77.70	6.48	10.42c	1.09d	0.07bcd	9.49d	6.75c	9.61bc
2012	–	–	–	15.19a	1.41ab	0.10b	10.77a	7.78a	11.37a
FYM									
1998	14.45	78.78	6.78	10.54c	1.09d	0.07bcd	9.64bcd	6.75c	9.23bcd
2012	–	–	–	14.36ab	1.29bc	0.10bc	11.12a	7.26b	9.87bc
GWS									
1998	14.98	78.35	6.68	10.29c	1.08d	0.07bcd	9.52cd	6.75c	9.13cd
2012	–	–	–	15.31a	1.47a	0.17a	10.42abc	6.93c	10.34ab
MSW									
1998	15.58	77.83	6.60	10.32c	1.09d	0.07bcd	9.42d	6.67c	9.36bcd
2012	–	–	–	12.49b	1.14cd	0.06cd	10.95a	7.45b	10.11bc
TEM									
1998	15.63	77.83	6.55	10.39c	1.12cd	0.08bcd	9.25d	6.8c	9.71bc
2012	–	–	–	9.34c	0.89e	0.05d	10.5ab	6.66c	8.29d

*** Significant at the 0.001 probability level.
† Values with the same lower case letters in a column are not significantly different at $P < 0.05$.

Table 3
Soil physico-chemical parameters from Colmar according to organic waste products applied and sampling time.[†]

Treatment	Clay	Silt	Sand	Organic carbon***	N***	P_2O_5 (Olsen)***	C:N***	pH (water)***	CEC***
	g kg^{-1}			g kg^{-1} DM					cmol + kg^{-1} DM
BIO									
2000	19.85	71.13	9.01	14.05a	1.34a	0.07b	10.47cd	8.25b	15.22bc
2012	–	–	–	14.7a	1.31ab	0.05ef	11.22abc	8.3ab	16.12a
FYM									
2000	22.43	68.95	8.63	13.77a	1.31ab	0.07bcd	10.53cd	8.28ab	15.05c
2012	–	–	–	14.82a	1.28ab	0.05de	11.60a	8.31ab	15.95abc
FYMc									
2000	19.69	71.07	9.25	13.2a	1.3ab	0.07b	10.15d	8.26ab	15.12c
2012	–	–	–	14.17a	1.23ab	0.06cde	11.50ab	8.31ab	15.97abc
GWS									
2000	21.39	70.53	8.08	13.85a	1.32ab	0.07ab	10.56bcd	8.23b	15.2bc
2012	–	–	–	14.7a	1.28ab	0.09a	11.42abc	8.25b	16.4a
SLU									
2000	21.06	69.68	9.25	14.22a	1.36a	0.07b	10.47cd	8.22b	15.12c
2012	–	–	–	14.35a	1.24ab	0.08ab	11.58a	8.26ab	16.12ab
TEM									
2000	21.19	69.52	9.30	14.92a	1.38a	0.07d	10.79abcd	8.24b	15.6bc
2012	–	–	–	13.67a	1.18b	0.04d	11.55a	8.35a	15.95f

*Significant at the 0.05 probability level.
**Significant at the 0.01 probability level.
*** Significant at the 0.001 probability level.
† Values with the same lower case letters in a column are not significantly different at $P < 0.05$.

2.3. High throughput sequencing of 16S and 18S rRNA gene sequences

For prokaryotic (bacterial-archaeal) diversity, a 440-base 16S rRNA fragment was amplified from each DNA sample (5 ng) with the corresponding primers: F479 (5′-CAG CMG CYG CNG TAA NAC-3′) and R888 (5′-CCG YCA ATT CMT TTR AGT-3′) as previously described (Tardy et al., 2014). For each sample, 5 ng of DNA were used for a 25 µL PCR conducted under the following conditions: 94 °C for 2 min, 35 cycles of 30 s at 94 °C, 52 °C for 30 s and 72 °C for 1 min, followed by 7 min at 72 °C.

For fungal diversity, a 350-base 18S rRNA fragment was amplified from each DNA sample (5 ng) with the corresponding primers: FF390 (5′-CGA TAA CGA ACG AGA CCT-3′) and FR1 (5′-ANC CAT TCA ATC GGT ANT-3′) (Chemidlin Prévost-Bouré et al., 2011). For each sample, 5 ng of DNA were used for a 25 µL PCR conducted under the following conditions: 94 °C for 3 min, 35 cycles of 30 s at 94 °C, 52 °C for 1 min and 72 °C for 1 min, followed by 5 min at 72 °C.

All PCR products were purified using the Agencourt® AMPure® XP kit (Beckman Coulter, Italy, Milano) and quantified with the Quantifluor (Promega, Lyon, France) staining kit according to the manufacturer's instructions.

A second PCR was performed with the purified PCR products (7.5 ng of DNA for bacteria and archaea, and 5 ng of DNA for fungi), with 10-bp multiplex identifiers added to the 5′ end of the primers for the specific identification of each sample and the prevention of PCR biases. For bacteria and archaea, the second PCR conditions were the same than previously described but with only seven cycles. For fungi, the second PCR conditions were optimized, with the number of cycles being reduced to seven and the denaturation step processed at 94 °C during 1 min. PCR products were purified with the MinElute gel extraction kit (Qiagen NV) and quantified with the Quantifluor (Promega, Lyon, France) staining kit according to the manufacturer's instructions. Equal amounts of each sample were pooled and then cleaned with the SPRI (Solid Phase Reverse Immobilization Method) using the Agencourt® AMPure® XP kit (Beckman Coulter, Italy, Milano). The pool was finally sequenced with a MiSeq Illumina instrument (Illumina Inc., San Diego, CA) operating with V3 chemistry and producing 250 bp paired-reads.

2.4. Bioinformatic analysis of 16S and 18S rRNA gene sequences

Bioinformatic analyses were done using the GnS-PIPE, which was initially developed by the Genosol platform (INRA, Dijon, France) (Terrat et al., 2012). First, all the 16S and 18S raw reads were sorted according to the multiplex identifier sequences. The raw reads were then filtered and deleted based on their length, their number of ambiguities (Ns), and their primer(s) sequence(s). More precisely, all raw sequences were checked and discarded if: (i) they contained any ambiguous base (Ns), (ii) if their length was less than 350 nucleotides for 16S reads or 300 nucleotides for 18S reads, (iii) if the exact primer sequences were not found (for the distal primer, the sequence can be shorter than the complete primer sequence, but without ambiguities). A PERL program was then applied for rigorous dereplication (i.e. clustering of strictly identical sequences). The dereplicated reads were then aligned using Infernal alignment (Cole et al., 2009), and clustered into operational taxonomic units (OTU) using a PERL program that groups rare reads to abundant ones, and does not count differences in homopolymer lengths. A filtering step was then carried out to check all single-singletons (reads detected only once and not clustered, which might be artifacts, such as PCR chimeras) based on the quality of their taxonomic assignments. Finally, in order to compare the datasets efficiently and avoid biased community comparisons, the reads retained were homogenized by random selection (17 649 and 21 726 reads for 16S and 18S rRNA gene sequences, respectively). Consequently, two samples from QualiAgro were discarded due to their low number of reads (one replicate of 16S CON and one replicate of 18S GWS). The prokaryotic and fungal rarefaction curves of the observed OTUs are presented in Supplementary Fig. S1.

The retained high-quality reads were used for: (*i*) taxonomy-independent analyses, determining several biodiversity indexes (Shannon, richness and evenness) and defining global OTU matrices, and (*ii*) taxonomy-based analysis using similarity approaches against dedicated reference databases from SILVA (Quast et al., 2012). The raw data sets are available in the EBI database system under project accession number PRJEB14258.

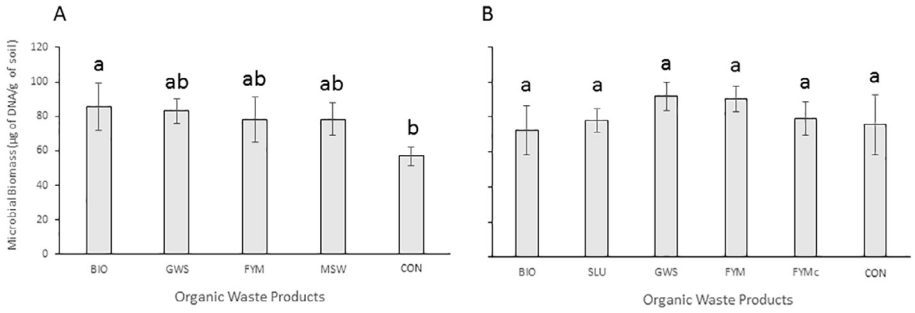

Fig. 1. Effect of different organic waste products on soil microbial biomass from QualiAgro (A) and Colmar (B).

2.5. Statistical analyses

All statistical analyses were carried out with R studio (RStudio, Version 0.98.501, RStudio Inc., Boston, Massachusetts, USA) using the free statistics software R (R version 3.0.2). OWP characteristics, soil physico-chemical characteristics, microbial biomass, microbial diversity indices and the relative abundance of prokaryotic, and fungal *phyla* in the microbial composition (i.e. inventory of present species) were processed by an analysis of variance. For soil physico-chemical characteristics only, the effect of organic waste product × sampling time was tested for each sampling site separately. For other parameters, only the effect of the organic waste product was tested for each sampling site separately. For all parameters, all significant effects were assessed by Tukey's Honestly Significant Difference (HSD) *post hoc* test ($P < 0.05$). All the variables were tested for normality using Shapiro-Wilk test. The prokaryotic and fungal communities (based on OTU matrices previously described) from all samples were also compared by using UniFrac (Lozupone and Knight, 2005), based on the 16S and 18S phylogenetic trees computed with FastTree (Price et al., 2010). Non-metric multidimensional scaling (NMDS) based on the Unifrac distance was used to visualize the patterns of distribution of microbial communities in relation to treatments. Similarities in the prokaryotic and fungal community structure (i.e. number and relative abundance of present species in the community) among treatments were investigated using an analysis of the similarity (ANOSIM) algorithm. To evaluate the effect of OWP, a distance-based redundancy analysis (dbRDA) approach was used. It was based on the Unifrac distance matrix and used to determine whether OWP had a direct and/or indirect effect on soil microbial community structure. In this approach, the indirect effect of OWP is mediated by modifications of soil properties, since OWP are recognized to modify soil properties (Diacono and Montemurro, 2010; Chalhoub et al., 2013). Therefore, it was first tested by evaluating the relative influence of environmental variables on soil microbial community structure. Then, the direct effect of OWP was tested by partialling out the effect of significant variables identified in the first step. For every statistical analysis, the significance threshold was set at $P < 0.05$.

3. Results

3.1. OWP physico-chemical characteristics

At QualiAgro, all composts (BIO, GWS and MSW) were characterized by larger dry matter contents (67.1 ± 9.6% of DM on average) and a smaller pH (7.7 ± 0.7 on average) than manure (39.6 ± 9.1% of DM on average and pH: 9.1 ± 0.3; Table 1). Organic matter quality varied among the different OWP. The MSW compost was characterized by a lesser potential efficiency to increase soil organic matter as shown by its smaller I_{ROC} (49%), compared to manure (FYM; 67%) and the two other composts (75 and 77%), which is related to the greater biodegradability of organic carbon observed for the MSW compost than for FYM manure and the two other composts (GWS and BIO) (Annabi et al., 2011). The C/N ratio was also significantly larger for MSW and FYM.

At Colmar, SLU, FYM and FYMc were characterized by low dry matter contents (18.9 ± 1.7% of DM on average; Table 1). SLU and GWS had a smaller pH (7.4 ± 0.6 on average) than the other amendments (9.2 ± 0.6 on average; Table 1). As observed for OWP from QualiAgro, organic matter quality also varied among OWP at Colmar. The SLU was characterized by greater biodegradability, and therefore smaller potential efficiency at increasing soil organic matter content (I_{ROC} 44%), than the other amendments (60–73%). In comparison to other amendments, SLU was also characterized by a smaller C/N ratio.

3.2. Soil physico-chemical characteristics

The soil texture at both experimental sites was similar, corresponding to a loamy clay (Tables 2 and 3). At QualiAgro, the soil organic carbon content in control plots did not change between 1998 and 2012 (Table 2). In 2012, soil chemical properties were found to be significantly modified in plots that had been repeatedly amended with OWP, showing an increase in organic carbon, N and P_2O_5 concentrations, pH value, and CEC, compared to control plots ($P < 0.001$; Table 2). However, the magnitude of these changes depended on the type of OWP, since the increase in soil organic carbon and N concentration was globally greater in plots amended with OWP with larger I_{ROC} (BIO and GWS).

At Colmar, the soil organic carbon content in control plots in 2000 and in 2012 was also similar (Table 3). In 2012, in contrast to QualiAgro, none of the five OWP inputs significantly modified soil chemical properties, except for P_2O_5 concentration, which was increased by all inputs ($P < 0.001$; Table 3).

3.3. Effects of organic amendment on microbial biomass, community structure and composition

At QualiAgro, BIO amendments significantly increased (50% higher) microbial biomass compared to control plots ($P < 0.01$; Fig. 1). At Colmar, no significant difference between the control and OWP-amended plots was apparent ($P > 0.05$; Fig. 1).

When each field site was considered separately, no significant effect of OWP on the soil microbial diversity indices (prokaryotic and fungi) was observed at either experimental site ($P > 0.05$; Table 4).

At QualiAgro however, analysis of similarity revealed a significant variation in the prokaryotic community structure among the five treatments ($R = 0.456$, $P < 0.001$). The NMDS ordination highlighted that the structure of the prokaryotic community in the control plots (CON) was different from those amended with BIO, GWS, FYM or MSW inputs (Fig. 2A). When only amended plots were considered, a difference in structure of the prokaryotic community was also observed between GWS and the other treatments (Fig. 2A). The prokaryotic community structure in MSW plots was similar to those of plots amended with BIO and FYM (Fig. 2A). The prokaryotic community structure in BIO and FYM plots was different (Fig. 2A). At the *phylum* level, the taxonomic composition of the prokaryotic community showed no

Table 4
Effect of different organic waste products on soil prokaryotic and fungal diversity indices from QualiAgro and Colmar.

Sampling site	Organic waste product							Effect of organic waste product[†]
	BIO	FYM	FYMc	GWS	SLU	MSW	TEM	
QualiAgro								
Prokaryote								
Richness	2148	1998	N/A	2200	N/A	2097	2001	NS
Shannon	5.44	5.01	N/A	5.34	N/A	5.2	5.14	NS
Evenness	0.71	0.66	N/A	0.69	N/A	0.68	0.68	NS
Density ($\times 10^9$ copies of 16S rRNA/g of soil)	4.15	4.96	N/A	6.26	N/A	3.24	1.94	NS
Fungi								
Richness	1644	1770	N/A	1504	N/A	1544	1616	NS
Shannon	4.66	4.64	N/A	4.53	N/A	4.34	4.66	NS
Evenness	0.63	0.62	N/A	0.62	N/A	0.59	0.63	NS
Density ($\times 10^9$ copies of 16S rRNA/g of soil)	3.65	3.89	N/A	5.23	N/A	4.17	2.61	NS
Fungal to bacterial ratio	0.0086a	0.0081b	N/A	0.0081b	N/A	0.0123a	0.0134a	*
Colmar								
Prokaryote								
Richness	1878	1833	1819	1840	1770	N/A	1822	NS
Shannon	5.0	4.98	5.13	4.98	4.78	N/A	5.04	NS
Evenness	0.67	0.66	0.68	0.66	0.64	N/A	0.67	NS
Density ($\times 10^9$ copies of 16S rRNA/g of soil)	5.85	6.38	4.22	6.52	5.61	N/A	4.3	NS
Fungi								
Richness	11,418	1105	1159	1135	1211	N/A	1135	NS
Shannon	4.06	4.01	4.13	3.89	4.03	N/A	3.88	NS
Evenness	0.58	0.57	0.59	0.55	0.57	N/A	0.55	NS
Density ($\times 10^9$ copies of 16S rRNA/g of soil)	3.69	4.48	1.84	5.2	3.27	N/A	4.25	NS
Fungal to bacterial ratio	0.0064	0.0084	0.0055	0.0079	0.0072	N/A	0.0098	NS

NS: Not Significant.
* Significant at the 0.05 probability level.
[†] Values with the same lower case letters in a row are not significantly different at $P < 0.05$.

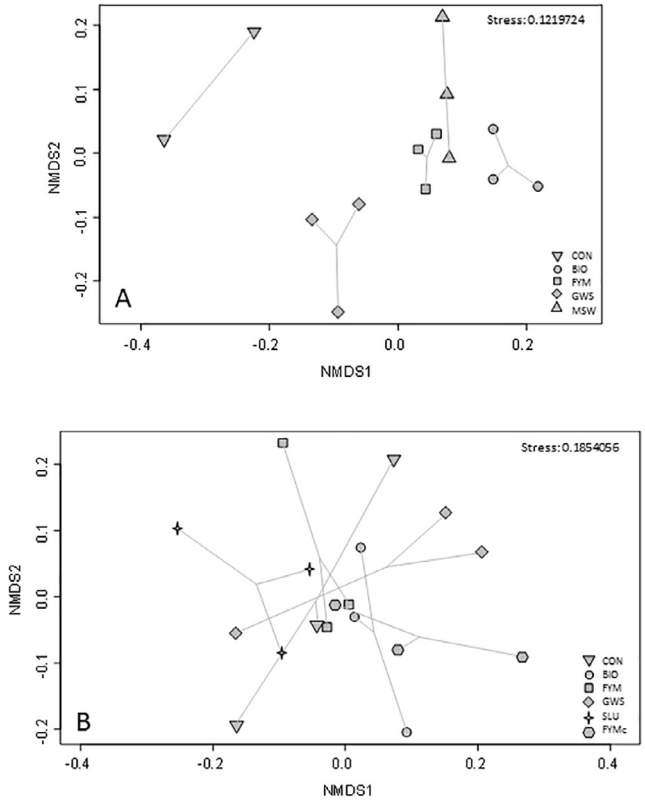

Fig. 2. Non-Metric Multi-Dimensional Scaling (NMDS) ordination plot derived from weighted pairwise Unifrac distances for prokaryotic community from QualiAgro (A) and Colmar (B).

difference between the control and amended plots ($P > 0.05$; Table 5). However, the prokaryotic community of soils amended with BIO contained more *Bacteroidetes* than soils amended with MSW ($P < 0.05$; Table 5). Besides for prokaryote, a significant variation between the five treatments was also found for the fungal community structure ($R = 0.492$, $P < 0.05$). The NMDS ordination highlighted that the fungal community structure in control plots (CON) differed from that of the BIO- or FYM-, and MSW-amended plots, but was close to the GSW-amended plots (Fig. 3A). When only amended plots were considered, a difference in structure of the fungal community was observed between MSW, GWS and BIO or FYM treatments. The fungal community structure in BIO plots was similar to that of plots amended with FYM (Fig. 3A). This finding was supported by the taxonomic composition at the *phylum* level, where *Basidiomycota* was significantly ($P < 0.01$) greater in control plots than in BIO and FYM, and *Glomeromycota* significantly ($P < 0.01$) greater in control plots than in GWS- and MSW-amended soils (Table 5).

At Colmar, analysis of similarity and NMDS ordination did not highlight any difference in the structures of the soil microbial communities between the control and amended plots (Figs. 2B and 3B). This was confirmed by the taxonomic composition at the *phylum* level, except for *Glomeromycota,* which was lesser in BIO-, GWS- and SLU-amended soils (Table 5, $P < 0.01$). *Chytridiomycota* was significantly ($P < 0.05$) greater in plots amended with FYMc than with SLU (Table 5, $P < 0.001$).

The dbRDA model analysis was used to test for direct and indirect (via modifying soil properties) effects of OWP on soil microbial community. At QualiAgro, OWP had a strong direct effect on prokaryotic community structure ($P < 0.001$; Supplementary Fig. S2) but also influenced this community structure indirectly by modifying soil pH ($P < 0.01$; Supplementary Fig. S2). Considering fungal community

Table 5
Relative abundance (%) of prokaryotic and fungal *phyla* (mean ± standard deviation) in microbial composition of soils from QualiAgro and Colmar according to organic waste product applied.

Phylum	QualiAgro					Colmar
	BIO	FYM	GSW	MSW	CON	BIO
Acidobacteria	5.28 ± 0.6	5.81 ± 0.42	5.92 ± 1.18	7.58 ± 1.09	6.04 ± 0.58	5.02 ± 0.34
Actinobacteria	3.82 ± 0.28	3.73 ± 0.21	5.04 ± 0.84	4.39 ± 0.66	4.66 ± 0.08	5.26 ± 0.33
Bacteroidetes	21.68 ± 2.91a	17.39 ± 2.59ab	15.91 ± 1.08ab	14.5 ± 2.31b	15.22 ± 3.18ab	14.15 ± 0.68
Chloroflexi	3.01 ± 0.3	2.56 ± 0.69	2.64 ± 0.28	2.51 ± 0.92	2.68 ± 0.66	2.14 ± 0.13
Crenarchaeota	5.35 ± 0.07	7.36 ± 1.01	7.2 ± 0.5	6.75 ± 0.84	8.77 ± 4.42	10.64 ± 0.44
Firmicutes	3.58 ± 0.31	3.76 ± 0.64	3.93 ± 0.41	3.87 ± 0.42	4.17 ± 0.16	4.67 ± 0.57
Planctomycetes	4.77 ± 0.33	4.47 ± 0.39	5.15 ± 0.51	5.17 ± 0.43	5.23 ± 0.95	6.51 ± 0.5
Proteobacteria	34.19 ± 1.5	29.67 ± 1.15	33.7 ± 1.81	32.45 ± 1.4	31.22 ± 5.37	28.81 ± 1.56
Thaumarchaeota	18.31 ± 1.79	25.26 ± 4.42	20.5 ± 0.85	22.78 ± 1.22	22.01 ± 5.75	22.8 ± 1.38
Ascomycota	43.21 ± 6.45	42.05 ± 7.87	38.57 ± 2.4	43.93 ± 4.35	37.12 ± 4.44	38.62 ± 3.01
Basidiomycota	17.2 ± 1.34bc	17.75 ± 1.57bc	20.26 ± 2.89ac	24.77 ± 3.48a	26.06 ± 2.27a	18.13 ± 1.4
Blastocladiomycota	1.34 ± 0.27	1.36 ± 1.04	0.93 ± 0.6	0.81 ± 0.49	0.92 ± 0.57	0
Chytridiomycota	11.06 ± 3.09	11.13 ± 3.74	7.31 ± 1.66	7.6 ± 0.54	6.6 ± 1.34	5.69 ± 0.36ab
Glomeromycota	2.01 ± 0.26ab	2.15 ± 0.66ab	1.8 ± 0.18b	1.43 ± 0.39b	2.97 ± 0.3a	1.23 ± 0.34b
Unknown	2.93 ± 0.2a	2.18 ± 0.36ab	2.52 ± 0.61ab	1.52 ± 0.15b	2.86 ± 0.45a	2.64 ± 0.35ab
Unclassified	9.43 ± 1.87	10.94 ± 3.48	12.64 ± 1.45	9.3 ± 1.83	9.67 ± 1.5	17.97 ± 0.48
Environmental	12.81 ± 0.85	12.45 ± 2.07	15.98 ± 3.65	10.64 ± 1.47	13.8 ± 0.61	15.72 ± 1.94

Phylum	Colmar					Effect of organic waste product[†]	
	FYM	FYMc	GSW	SLU	CON	QualiAgro	Colmar
Acidobacteria	5.08 ± 0.1	4.74 ± 1.46	4.16 ± 0.36	5.07 ± 0.47	5.89 ± 0.38	NS	NS
Actinobacteria	4.72 ± 0.71	5.41 ± 0.97	4.56 ± 0.14	4.69 ± 0.48	5.37 ± 0.94	NS	NS
Bacteroidetes	15.4 ± 1.02	17.67 ± 2.05	17.84 ± 4.21	13.69 ± 3.17	13.67 ± 3	*	NS
Chloroflexi	2.1 ± 0.59	1.86 ± 0.22	1.99 ± 0.19	1.82 ± 0.16	2.31 ± 0.14	NS	NS
Crenarchaeota	12.2 ± 1.53	9.25 ± 1.65	10.83 ± 2.47	11.52 ± 1.31	11.14 ± 3.43	NS	NS
Firmicutes	4.48 ± 0.23	5.05 ± 0.9	4.12 ± 0.59	3.92 ± 0.22	4.34 ± 0.58	NS	NS
Planctomycetes	6.3 ± 0.75	6.47 ± 0.33	6.2 ± 0.55	6.21 ± 0.23	6.88 ± 0.35	NS	NS
Proteobacteria	26.77 ± 1.5	30.86 ± 3.39	27.4 ± 2.42	26.55 ± 1.77	28.76 ± 3.57	NS	NS
Thaumarchaeota	22.95 ± 2.71	18.69 ± 2.95	22.89 ± 5.49	26.53 ± 4.16	21.63 ± 5.02	NS	NS
Ascomycota	41.59 ± 14.21	38.81 ± 2.19	45.2 ± 12.76	41.27 ± 6.19	44.96 ± 17.05	NS	NS
Basidiomycota	16.87 ± 3.95	15.63 ± 1.2	14.86 ± 2.18	20.27 ± 2.77	16.12 ± 4.8	**	NS
Blastocladiomycota	0	0	0	0	0	NS	NS
Chytridiomycota	4.63 ± 1.43ab	7.56 ± 2.21a	4.15 ± 0.73ab	3.95 ± 0.67b	4.47 ± 1.3ab	NS	*
Glomeromycota	1.86 ± 0.82ab	1.44 ± 0.05ab	1.34 ± 0.28b	1.3 ± 0.43b	2.72 ± 0.5a	**	**
Unknown	3.35 ± 0.05ab	3.46 ± 0.87a	2.27 ± 0.71ab	2.11 ± 0.29ab	2.06 ± 0.26b	**	*
Unclassified	17.08 ± 4.67	19.08 ± 2.19	18.63 ± 8.0	14.18 ± 1.46	17.22 ± 7.59	NS	NS
Environmental	14.63 ± 3.62	14.03 ± 1.77	13.56 ± 2.5	16.92 ± 2.65	12.45 ± 3.11	NS	NS

NS: Not Significant.
* Significant at the 0.05 probability level.
** Significant at the 0.01 probability level.
[†] Values with the same lower case letters in a row and within a research site are not significantly different at $P < 0.05$.

structure, only a direct effect of OWP was detected ($P < 0.001$; Supplementary Fig. S2). At Colmar, in agreement with the NMDS and the lack of soil properties modifications, no effect of OWP on prokaryotic and fungal community structure was detected.

4. Discussion

As a result of human activities, large quantities of organic wastes are produced, such as animal manures or sewage sludge, which need to be recycled in order to minimize adverse environmental impact. One promising option is to use these OWP in agriculture as amendments to increase soil fertility, since they can constitute nutrient sources for crops. To better understand how OWP might increase soil fertility, we assessed the lasting effect on soil microbial communities of applications of different types of organic fertilizers repeated for more than 10 years.

At QualiAgro, seven months after the 7th OWP application, an increase in soil microbial biomass was observed in BIO-amended plots. This is in accordance with Ros et al. (2006), who highlighted an increase in microbial biomass 5 months after a repeated organic fertilization over several years. BIO amendment produced the greatest increase in soil pH. As observed by Zhalnina et al. (2015), in the present study, a positive correlation between soil pH and soil microbial biomass was observed at QualiAgro ($r = 0.534$, $P < 0.05$). This suggests that several years of BIO application led to a lasting increase in soil pH, allowing optimum growth of soil microbes, and thus an increase in soil microbial biomass (Rousk et al., 2010).

The microbial diversity indices (prokaryotic and fungi) recorded in amended plots were similar to those of control plots, despite the increase in microbial biomass. This was not in accordance with previous studies highlighting 4–5 months after the last OWP application, an increase of bacterial (Parham et al., 2003; Ros et al., 2006; Chen et al., 2016), but a decrease of fungal diversity and richness indices (Chen et al., 2016). In the present study, the delay between the last OWP application and soil sampling was probably too long (7 months) to see a lasting effect of OWP on soil microbial diversity indices. In addition, as pointed out by Hartmann et al. (2015), the difference of results observed between our work and these studies could be due to the variation of the methods used (sequence of primers, bioinformatics analysis, etc.), on the metric itself, and, largely, on the experimental design.

At QualiAgro, seven months after a repeated application of OWP, the structure of the prokaryotic community in amended plots differed from that of the control. This was directly the consequence of the OWP applied and indirectly a consequence of a lasting modification of soil properties. As suggested by Saison et al. (2006), microorganisms present in the organic materials added to soil are rapidly outcompeted by soil-derived microorganisms and therefore only marginally influence changes in community structure. Thus, the direct effect OWP applied would be mainly due to the physic-chemical characteristics of amendment rather that to amendment-borne microorganisms (Saison et al., 2006). Concerning the indirect effect of OWP, our results highlighted that soil pH was a major driver of soil prokaryotic community structure. This was consistent with previous studies that indicated pH as the main factor that influenced microbial community composition in agro-ecosystems (Hartman et al., 2008; Lauber et al., 2008; Zhalnina et al., 2015; Francioli et al., 2016; Kaiser et al., 2016). A number of mechanisms may account for the link between pH and prokaryotic community structure, as soil pH may select some microbial taxa over others (Rousk et al., 2010), besides affecting nutrient availability (Kemmitt et al., 2006).

In the present study, contrastingly to results obtained on prokaryotic community structure, no lasting effect of OWP on the taxonomic composition of this community was observed at the *phylum* level. Indeed, at this high taxonomic rank, no major effect on microbial communities was detected, although some minor changes where measured in some *phyla* at the OTU level. Ours results were however, not in accordance with Chen et al. (2016), who observed changes in the

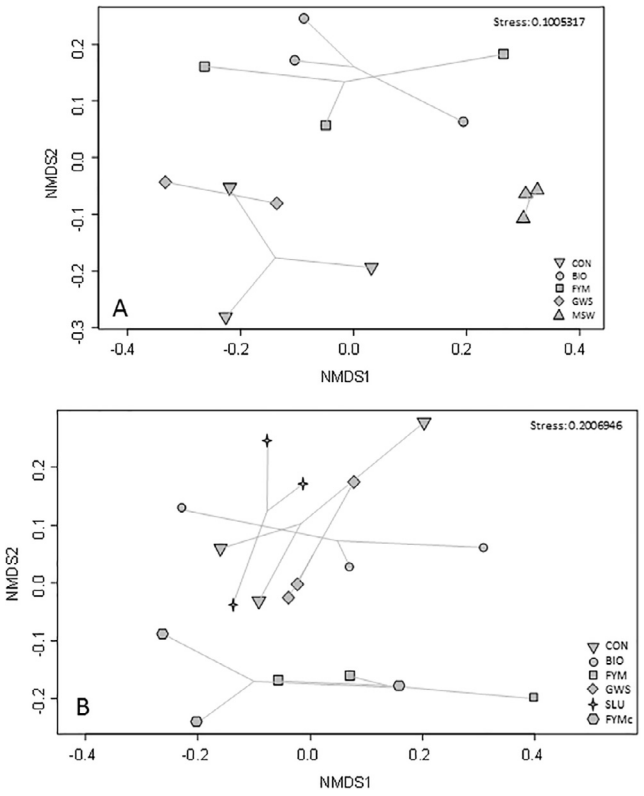

Fig. 3. Non-Metric Multi-Dimensional Scaling (NMDS) ordination plot derived from weighted pairwise Unifrac distances for fungal community from QualiAgro (A) and Colmar (B).

bacterial community structure and composition 4 months after the last application of organic fertilizer in a long-term experiment. Particularly, these authors observed variation in relative abundance in the bacterial *phyla Acidobacteria*, *Gemmatimonadetes* and *Cyanobacteria*, most of which were correlated with soil organic matter and/or nitrate N (NO_3^--N) content (Chen et al., 2016).

At QualiAgro, the change in structure of the fungal community was still apparent seven months after a repeated application of OWP. This effect was OWP-dependent, but weaker than for prokaryote, since only three out of four treatments (BIO, FYM and MSW) were discriminated from the control. This confirmed previous reports suggesting that soil bacteria seem to be a more sensitive indicator of soil fertility than soil fungi (Zhong et al., 2010). In opposition to the prokaryotic community, no soil physico-chemical parameters have been identified as major driver affecting the structure of the soil fungal community. This was not in accordance with Francioli et al. (2016), who observed that soil fungal community structure was driven by soil pH, phosphorus and nitrogen. In our case, no influence of these three parameters on fungal community structure was found, probably because the applied amendments were different, and/or the duration of OWP application was shorter than in the Francioli's study (14 years *vs* > 100 years).

Contrary to the prokaryotic community, repeated applications of OWP also induced lasting changes in fungal community composition at the *phylum* level. Globally, the application of OWP tented to increase *Basidiomycota*, one of the main soil decomposers (Ma et al., 2013; Weber et al., 2013) and decrease *Glomeromycota*. According to Egerton-Warburton and Allen (2000), the N enrichment by OWP application may cause a reduction in spore abundance leading to the decrease of *Glomeromycota* observed.

Surprisingly, 15 months after the last OWP application, the soil physico-chemical parameters in the control and amended plots at Colmar were similar, despite 6 repeated OWP applications within 12 years. This is mirrored by the microbial community parameters,

since a repeated application of OWP did not have any lasting effect on soil microbial biomass, diversity or structure. In addition, as observed for QualiAgro, the OWP had only a slight effect on soil fungal composition at the *phylum* level, with a decrease of *Glomeromycota* after soil applications of SLU, GWS or BIO. This was consistent with Crecchio et al. (2004) and Poulsen et al. (2013a), who did not observed major changes in bacterial community 9 months after 6 and 4 years of a repeated organic fertilization, respectively. In contrast, after more than 21 years of a repeated application, Francioli et al. (2016) and Zhong et al. (2010), observed a lasting (12 months) effect of OWP on soil microbial communities. More precisely, these authors observed, after the last organic fertilizer application, a stimulation of different bacterial *phyla* (*Firmicutes* and *Proteobacteria*) that are known to prefer nutrient-rich environments, and are involved in the degradation of complex organic compounds (Francioli et al., 2016). All of these results suggested that 6 years of repeated OWP application remained not sufficient to lasting modify soil microbial community more than 12 months. Other hypotheses could explained the fact that the soil in Colmar responded less to OWP applications than the soil in QualiAgro. This might be because the OWP at Colmar were applied at a lower rate than at QualiAgro (~ 1.7 Mg C ha^{-1} *vs* ~ 4 Mg C ha^{-1} respectively), and/or the difference observed between the native soil organic matter content of both field experiments. Indeed, before starting the long-term experiment, the soil organic matter content at QualiAgro (1.79 ± 0.1 g kg^{-1} DM) was significantly lower than at Colmar (2.41 ± 0.1 g kg^{-1} DM). As observed by Yanardağ et al. (2017), native soil organic matter determined the response of microbial communities to external inputs, soils with lower organic matter being more prone to increase microbial biomass and change microbial community structure.

5. Conclusions

The present study indicated that a repeated OWP applications lastingly modified the physico-chemical status of soil, with a parallel increase in soil microbial biomass and a change of microbial community structure. Our results suggested that this lasting effect of OWP on soil microbial communities would depended on: (i) the duration of OWP repeated application (more than 10 years), (ii) the rate (here ~ 4 Mg C ha^{-1}) of OWP applied and (iii) the delay between OWP application and soil sampling (the lasting effect observed 7 months after the last application may end after 15 months). Our study also showed that the effects on soil physico-chemical parameters and microbial communities were impacted by the quality of the different OWP applied.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.apsoil.2018.02.006.

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