Biology and Fertility of Soils (2024) 60:525–545
https://doi.org/10.1007/s00374-024-01813-0

ORIGINAL PAPER

Potato yield and quality are linked to cover crop and soil microbiome, respectively

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Received: 4 July 2023 / Revised: 9 March 2024 / Accepted: 11 March 2024 / Published online: 4 April 2024

Abstract

Crop-specific cultivation practices including crop rotation, cover cropping, and fertilisation are key measures for sustainable farming, for which soil microorganisms are important components. This study aims at identifying links between agronomic practices, potato yield and quality as well as soil microorganisms. We analysed the roles of cover crops and of the soil prokaryotic, fungal, and protistan communities in a long-term trial, differing in crop rotation, i.e. winter wheat or silage maize as pre-crop, presence and positioning of oil radish within the rotation, and fertilisation, i.e. mineral fertiliser, straw, manure, or slurry. Up to 16% higher yields were observed when oil radish grew directly before potatoes. Losses of potato quality due to infection with *Rhizoctonia solani*-induced diseases and common scab was 43–63% lower when wheat + oil radish was pre-crop under manure or straw + slurry fertilisation than for maize as pre-crop. This contrast was also reflected by 42% higher fungal abundance and differences in β-diversity of prokaryotes, fungi, and protists. Those amplicon sequence variants, which were found in the treatments with highest potato qualities and differed in their abundances from other treatments, belonged to Firmicutes (2.4% of the sequences) and Mortierellaceae (28%), which both comprise potential antagonists of phytopathogens. Among protists, Lobosa, especially *Copromyxa*, was 62% more abundant in the high potato quality plots compared to all others, suggesting that specific higher trophic organisms can improve crop performance. Our findings suggest that successful potato cultivation is related (1) to planting of oil radish before potatoes for increasing yield and (2) to fertilisation with manure or straw + slurry for enriching the microbiome with crop-beneficial taxa.

Keywords Common scab · Crop rotation · *Helminthosporium solani* · Oil radish · *Rhizoctonia solani* · Silver scurf

Introduction

Potatoes (*Solanum tuberosum* L.) play an important role in a healthy human diet (Camire et al. 2009) and were the fourth most produced food crop in 2021 (www.fao.

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org/faostat/). However, potatoes have a high demand for fertilisers and are susceptible to a wide range of pathogens and pests, often necessitating pesticide treatments (Wu et al. 2013). Among the soil-borne pathogens and pests acting on potatoes, Fiers et al. (2012) listed 30 genera of bacteria, fungi, protists, and nematodes. Furthermore, there are viruses and arthropod larvae like wireworms (Elateridae), which reduce potato yield and quality (Fiers et al. 2012). Reported potato yield losses due to pathogens were 100% by the common scab-inducing actinobacteria *Streptomyces* spp. (Charkowski et al. 2020), up to 47% by the ascomycete *Colletotrichum coccodes* (Wallr.) S. Hughes (Daami-Remadi et al. 2010), and 30% by the dry core-inducing basidiomycete *Rhizoctonia solani* J.G. Kühn (Tsror 2010). Blemishes like common scab, black dots (*C. coccodes*), black scurf (*R. solani*), and silver scurf (ascomycete *Helminthosporium solani* Durieu & Mont.) only damage the skin. Consequently, they do not induce yield reduction like for *H. solani* (Errampalli et al. 2001), but severely reduce the economical value of potatoes (Fiers et al. 2012).

Crop rotation counteracts decreases in yield and quality associated with monocultures over time. A diverse crop rotation not only increases yields (Blecharczyk et al. 2023; Larkin et al. 2021; Scholte 1990; Wright et al. 2017), but also decreases negative effects on quality (Larkin and Honeycutt 2006) as well as disease incidents, i.e. abundance of affected plants or their marketable parts, and severity, i.e. the extent of damage (Larkin and Honeycutt 2006; Wright et al. 2017). For the crop at the end of the rotation, its performance depends on the choice of the preceding one (Honeycutt et al. 1996; Mohr et al. 2011; Specht and Leach 1987).

Cover cropping is an important means to support cash crops like potatoes. Cover crops, also referred to as catch crops, take up soil nitrogen (N) with Brassicaceae like oil radish, trapping up to 200 and more kg N ha^{-1} (Justes 2017). As 40–60% of plant biomass N derives from soil organic matter (Tonitto et al. 2006), decayed cover crops play an important role in nutrient management of subsequent cash crops (Wilson et al. 2019). They also increase stocks of soil organic carbon (Poeplau and Don 2015), thus, improving soil physical conditions for cash crop growth (Kaspar and Singer 2011). Overall, cover crops can lead to increased cash crop yields (Marcillo and Miguez 2017; Osipitan et al. 2018), though the effectiveness depends on agronomic practices like fertilisation (Justes 2017). Control of pests and phytopathogens is a further function (Kaspar and Singer 2011; Tiwari et al. 2022), as inclusion of cover crops can disrupt epidemic cycles by reducing receptiveness of the soil and by allelopathic bio-fumigation (Justes 2017). For instance, Brassicaceae cover crops are known to reduce severity of common scab in potatoes (Charkowski et al. 2020; Tiwari et al. 2022).

The soil microbial community comprising, e.g., prokaryotes, fungi, and protists, provides ecosystem services supporting cash crops. Growth of microorganisms improves soil conditions by aggregation (Oades and Waters 1991; Tisdall and Oades 1982). Microorganisms release plant available nutrients by weathering of minerals (Gadd 2007; Uroz et al. 2009) and by degrading soil organic matter (Krishna and Mohan 2017) or provide nutrients to plants such as by N_2 fixation, phosphorus (P) solubilisation or production of iron chelating siderophores (Bhattacharyya and Jha 2012; Vukicevich et al. 2016). Plant growth-promoting rhizobacteria (PGPR), fungi, and oomycetes (both PGPF) as well as mycorrhizal fungi can enhance plant growth by production of phytohormones, relieve of stress or induction of stress tolerance, and induction of immune responses, which strengthens the plants' resistance and defence against pathogens (Akhtar and Siddiqui 2010; Bhattacharyya and Jha 2012; Hossain et al. 2017; Vukicevich et al. 2016). Microorganisms further suppress phytopathogens by competition for nutrients and colonisation sites (Jayaraman et al. 2021), by production of antibiotics (Akhtar and Siddiqui 2010; Deveau et al. 2018; Rodrigo et al. 2021), and by parasitising or preying (Geisen et al. 2018; Olanya and Lakshman 2015; Velicer and Mendes-Soares 2009; Vukicevich et al. 2016). Higher trophic-level protists control these processes by predation and they also directly benefit plants by liberating nutrients via the microbial loop (Geisen et al. 2018). Depending on the microbial community, soils can become disease suppressive or conducive. Suppressive soils harbour higher microbial biomass, biodiversity, and activity than non-suppressive soils (Chandrashekara et al. 2012; Jayaraman et al. 2021), which can be strongly altered by management, fertilisation (Hemkemeyer et al. 2015; Schwalb et al. 2023b; Zhao et al. 2019), and cover cropping (Finney et al. 2017; Kim et al. 2020).

In the current study, we compared different potato cultivation methods, which aim at increasing yield and quality. For this reason, we analysed soil abiotic and microbial factors in order to explain the link between agronomic approaches, soil microorganisms, and potato production. The Pfalzdorf long-term potato trial, which ran from 2001 to 2019 in the Lower Rhine region, Germany, employed different crop rotations, i.e. winter wheat or silage maize as pre-crop as well as presence and positioning of oil radish within the rotation, and fertilisation types, i.e. mineral fertiliser, straw, manure, or slurry. We hypothesised that those combinations of crop rotation and fertilisation, which led to highest potato yields and qualities in terms of lowest disease incidences, (1) had positioned the cover crop directly before potatoes. These combinations further led to soils containing (2) higher amounts of nutrients and higher microbial (3) abundances, (4) activities, and (5) diversity. Furthermore, they led to (6) microbial communities harbouring more potentially

beneficial taxa in terms of plant growth promotion and disease suppression.

Materials and methods

Study site and experimental design

The study site was located in the Lower Rhine region in Germany (51°43′7.6"N, 6°09′18.1"E, 15 m above sea level) on a loess-derived Stagnic Luvisol with silty loam texture (18.5% 63–2000 µm, 72.3% 2–63 µm, 9.2% < 2 µm). During the trial, mean annual precipitation and temperature was 770 mm and 10.9 °C, respectively (Berendonk 2020). The trial ran from 2001 until 2019 starting with potato (cultivar Marabel) as initial crop followed by six full three-year crop rotation cycles (Table 1). The treatments differed in the positioning of the cash crops winter wheat (*Triticum aestivum* L., different cultivars with Ornica being last) and silage maize (*Zea mays* L., different cultivars with Oldham being last) and the cover crop oil radish (*Raphanus sativus var. oleiformis* Pers., cultivar Adios) within the crop rotation. Furthermore, there were differences in tillage (absence or timing of ploughing) and fertilisation (mineral fertiliser, shredded straw, cattle manure, pig slurry).

The amounts of N applied depended on the content of inorganic N in the soil and potential delivery from litter decay to reach target values of N content in the soil of 140 kg ha^{-1} for potatoes, 210 kg ha^{-1} for winter wheat, 190 kg ha^{-1} for maize, and 40 kg ha^{-1} (mineral fertiliser) or 80 kg ha^{-1} (manure/slurry) for oil radish. Similarly, basic mineral fertilisation of all treatments with P, potassium (K), magnesium (Mg), and calcium (Ca) depended on respective contents and pH in 0–30 cm of soil. For details of fertiliser application see Berendonk (2020). Seven treatments (T1–T8 with T3 not being sampled) were arranged in a randomised block-design with four replicates at a plot size of 9 × 9 m^2. The composition of the factors crop rotation, fertilisation, and tillage in the treatments was not factorial, but the treatments followed common farming practices of the region (Table 1). As plant protection differed between maize and wheat and, in accordance to needs, between years, treatments T1–T6 (wheat as pre-crop) and T7–T8 (maize as pre-crop) received different types and amounts of pesticides, while within each group of treatments plant protection was the same; it was also similar for potatoes, the most intensively managed crop in the crop rotations (see Supplementary Table S1).

Table 1 Three-year crop rotation cycle with factors differing between treatments (T). Management of cash crops and cover crops are highlighted by grey and blank background, respectively

	T1	T2	T4[a]	T5	T6	T7	T8
Ploughed	Yes	Yes	Yes	Yes	Yes	No	No
Fertilisation	Mineral	Mineral	Mineral	Mineral	Slurry	Mineral	Mineral
Cash crop I	Silage maize	Silage maize	Silage maize	Silage maize	Silage maize	Winter wheat	Winter wheat
Ploughed						Yes	Yes
Fertilisation						Mineral	Mineral
Cover crop	–[b]	–[b]	–[b]	–[b]	–[b]	Oil radish	Oil radish
Ploughed	Yes	Yes	Yes	Yes	Yes	No[c]	No[c]
Fertilisation	Mineral	Mineral	Mineral	Mineral	Mineral	Mineral	Mineral
Cash crop II	Winter wheat	Winter wheat	Winter wheat	Winter wheat	Winter wheat	Silage maize	Silage maize
Ploughed		Yes	No	No	No		
Fertilisation		Mineral	Mineral+straw[d]	Manure[d]	Straw+slurry[d]		
Cover crop	Fallow	Oil radish	Oil radish	Oil radish	Oil radish	Fallow	Fallow
Ploughed	Spring	No[c]	Spring	Spring	Spring	Autumn	Spring
Fertilisation	Mineral	Mineral	Mineral	Mineral	Slurry	Mineral	Mineral
Cash crop III	Potato	Potato	Potato	Potato	Potato	Potato	Potato
Times ploughed per crop rotation	3	3	3	3	3	2	2
Times fertilised per crop rotation	3	4	4	4	4	4	4

[a] Treatment T3 was not sampled.
[b] Winter wheat was growing since mid-autumn.
[c] If oil radish had not been killed by frost, 2 L ha^{-1} glyphosate was applied.
[d] Incorporated into soil by rotary harrow or spike drum.

Potato harvest and quality assessment, long-term soil sampling

Potatoes were harvested in autumn and yield was determined after each crop rotation cycle, i.e. not for the initial year 2001. At time of the establishment of the field trial, it was common practice to determine potato yield as fresh weight and it is still an important determinant for the market prize. Due to this legacy and the practice-orientation of the trial, only fresh weights were determined, even though dry weights should be reported in future trials (Bashan et al. 2017). Potato quality was determined by assessing 100 randomly picked potatoes per replicate visually for tuber deformations, and traits induced by different fungal, bacterial, and faunal pests. In 2016 and 2019 only 25 potatoes per replicate were picked in accordance with the Federal Plant Variety Office but scaled up to 100 to enable comparison. Assessments of the different quality traits started in different years depending on their first appearance.

Accompanying destructive soil sampling took place in autumn of each year from the first 30 cm in order to determine long-term soil nutrient concentrations. The field replicates of each year of these long-term soil samples were combined prior to analyses and sent cooled at + 5 °C to the LUFA Münster, Germany, for analysis. As this combining had led to a loss of field variability, only variability in time could be considered and, thus, the long-term nutrient results are of limited explanatory power.

Soil sampling in 2019 and 2015 and basic soil parameters

For microbial properties and contemporary soil nutrient concentrations, soil sampling took place in October 2019, two days after harvest of the potatoes. Earlier samplings were conducted in February 2015 under young winter wheat (T1–T6) or oil radish (T7–T8) as preceding vegetation and, for molecular genetic analyses only, in May 2019 shortly after seeding of the potatoes with fallow after winter wheat (T1) and maize (T7–T8), respectively, or oil radish (T2–T6) as preceding vegetation. In May 2019 the ridges were sampled from the top down to the level of the furrows without harming the seeding potatoes, while in 2015 and in October 2019 the first 10–15 cm were sampled to account for the levelling of the former ridges. Per replicate, 30 subsamples were taken across a plot, pooled, and homogenised during sieving to < 2 mm. The samples were either stored at + 4 °C until further analysis or, for 2015 and May 2019 samples, frozen at -20 °C for molecular genetic analysis.

Water holding capacity was determined according to Wilke (2005). For pH measurement the soil was manually stirred at 5 min intervals in a 0.01 M $CaCl_2$ solution at a ratio of 1:2 (w/v) and measured after 30 min (2015 samples: 1:5 (w/v) in distilled water). For total carbon (C), N, and sulphur (S) determination soil was milled and dry combusted at 900 °C in a Vario Max Cube CHNS (Elementar, Langenselbold, Germany). For extractable soil elements see below.

Incubation experiment, activity measurements, and water-stable aggregates

After moistening the soil up to 50% of its water holding capacity, a 100 g fresh weight sample in a 1-L-bottle and further 10 g in a 100-mL-bottle were pre-incubated at 22 °C in the dark for 7 d. Afterwards the 10 g sample was stored frozen (-20 °C) until determination of inorganic N (t_0). The 1-L-bottle was supplied with a vial containing 10 mL 0.5 M NaOH and incubated for a further 7 d to determine basal respiration. Soil from this incubation was used to measure soil extractable and microbial elements (see below) and, after storage at -20 °C, inorganic N (t_1), water-stable aggregates, and molecular parameters were measured. For the 2015 samples the incubation conditions were as following: 3 d pre-incubation, 35 d main incubation, and exchange of alkali traps every 7 d with reduction of NaOH concentration to 0.25 M after 14 d; measurements were constrained to basal respiration and soil extractable and microbial biomass C and N.

Inorganic N, i.e. the sum of NH_4^+-N, NO_2^--N, and NO_3^--N, was measured using a continuous segmented flow analyser (AA3, SEAL Analytical, Norderstedt, Germany) and net N mineralisation within 7 d was calculated as:

$$\delta N_{min}\left[\mu g \cdot g^{-1} d^{-1}\right] = \frac{N_{min,t_1} - N_{min,t_0}}{7d} \quad (1)$$

For basal respiration, the alkali traps were back-titrated with 0.1 M HCl according to Pell et al. (2006) using Titro-Line 6000 (SI Analytics, Mainz, Germany). Basal respiration divided by soil microbial biomass C resulted in the metabolic quotient (qCO_2).

Water-stable aggregates of replicates B–D were determined after air-drying and sieving to > 1 mm in a wet-sieving apparatus (Eijkelkamp, Giesbeek, The Netherlands) according to the manufacturer. In brief, a mass of 4 g soil was wetted with distilled water using a sprayer and left to soak for 5 min. Subsequently, the sample was wet-sieved with mesh-size 250 µm at 34 strokes per minute, first in distilled water for 3 min (W_{H2O}) and subsequently in 0.05 M NaOH for 5 min (W_{NaOH}). After drying at 105 °C, water-stable aggregates (WSA) were calculated as:

$$WSA[\%] = \frac{W_{\mathrm{NaOH}} - W_{NaOH,empty} - m_{NaOH}}{W_{NaOH} - W_{NaOH,empty} - m_{NaOH} + W_{H_2O} - W_{H_2O,empty}} \cdot 100\% \quad (2)$$

with $W_{NaOH, empty}$ and $W_{H2O, empty}$ being the respective empty weights of the vessels and m_{NaOH} being the mass of NaOH used in the vessel.

Soil microbial and extractable elements

Microbial biomass C, N, and P were determined by fumigation-extraction according to Vance et al. (1987), Brookes et al. (1985), and Brookes et al. (1982), respectively, with conversion values 0.45 (Joergensen 1996), 0.54 (Joergensen and Mueller 1996), and 0.40 (Brookes et al. 1982), respectively. Further chloroform-labile elements, i.e. microbial derived elements for which conversion values are not yet available, were extracted with 0.01 M $CaCl_2$ at 1:20 (w/v) ratio and shaking at 200 rpm for 1 h (Schwalb et al. 2023a). While C and N were analysed in the Multi C/N 2100 S analyser (Analytic Jena, Jena, Germany), P and other elements were measured in an inductively coupled argon plasma optical emission spectrometer (ICP-OES, Optima 8000, Perkin Elmer, Waltham, USA). Due to the low microbial biomass, only for manganese (Mn) reliable data were obtained among the chloroform-labile elements. However, all extracts of the non-fumigated samples were considered as extractable, i.e. easily bioavailable, elements including C, N, and P. Elemental ratios were calculated on a molar and not on a mass base (Schwalb et al. 2023b).

DNA extraction and quantitative real-time PCR

Genomic DNA was extracted using the FastDNA™ SPIN Kit for Soil and FastPrep®-24 bead-based homogeniser (both MP Bio, Santa Ana, USA). The extraction protocol was slightly modified according to Hemkemeyer et al. (2014) by adjusting volumes of sodium phosphate buffer and supplied "MT" to 950 µL and 120 µL, respectively. The bead-beater was run twice at 6.5 m s^{-1} for 45 s. Furthermore, DNA bound to the glass milk was additionally washed two times, using 1 mL 5.5 M guanidine thiocyanate to reduce soil contaminants. Finally, eluate obtained with 100 µL distilled water was added back to the column to elute a second time to increase elution efficiency. DNA lost during the extraction process, i.e. remaining in pellets and non-transferred supernatants, was accounted for by dividing gene copy numbers (see below) by k_{DNA}:

$$k_{DNA} = \frac{(c-d)\cdot\frac{c-b}{c-a}}{m_s\cdot\frac{u}{100\%+u}+m_{spb}+m_{MT}} \quad (3)$$

with a = mass of empty reaction tube; b = mass of tube and added supplied "PPS"; c = mass of tube, "PPS", and added crude DNA extract; d = mass of tube after centrifugation and removing supernatant; m_s = soil sample fresh weight; u = gravitational soil water content in %; m_{spb} = mass of sodium phosphate buffer; m_{MT} = mass of "MT" buffer.

Quantification of microbial abundances was done in the Light Cycler 480® II (Roche Diagnostics, Mannheim, Germany), using the Light Cycler 480® Probes Master for bacterial 16S rRNA genes (primers BAC338F and BAC805R and probe BAC516F) and archaeal 16S rRNA genes (primers ARC787F and ARC1059R and probe ARC915F) (Yu et al. 2005). Fungal ITS1 sequences were quantified using LightCycler® 480 SYBR Green I Master with the primers NSI1 and 58A2R (Martin and Rygiewicz 2005). Reaction mixtures, cycling conditions, and, in case of fungi, conditions of melting curve analysis have been published with open access elsewhere (Wichern et al. 2020). For 2019 samples the standard curve was prepared from amplicons derived from *Bacillus subtilis* (bacteria), *Methanobacterium oryzae* (archaea), and *Fusarium graminearum* (fungi) and inserted into a plasmid using the pGEM®-T Vector System II Kit (Promega, Madison, USA). In the case of 2015 samples, amplicons derived from environmental samples without insertion into a plasmid. Efficiencies (Eff) of the qPCR calculated as:

$$Eff = \left(10^{-\frac{1}{m}} - 1\right)\cdot 100\% \quad (4)$$

with m = slope of the standard curve are given in the Supplementary Table S2.

Illumina MiSeq sequencing and bioinformatic analyses

Aliquots of the 2019 samples' DNA extracts were lyophilised prior to library preparation. The V4 region of the 16S rRNA gene was PCR-amplified to investigate prokaryotic communities using the primer set 515F (GTGYCA GCMGCCGCGGTAA) and 806R (GGACTACNVGGG TWTCTAAT) (Caporaso et al. 2011). Meanwhile, the V4 region of the 18S rRNA gene was broadly targeted to investigate eukaryotic communities using the primer set V4_1f (CCAGCASCYGCGGTAATWCC) and TAReukREV3 (ACTTTCGTTCTTGATYRA) (Bass et al. 2016). PCR was performed in a 20 µl volume consisting of 4 µl of 5× reaction buffer, 2 µL dNTPs (2.5 mM), 0.8 µL of each primer (10 µM), 0.4 µL FastPfu Polymerase, 10 ng of DNA template, and the rest being ddH_2O. Amplification was performed with the following temperature regime: 5 min of initial denaturation at 95 °C, followed by 30 cycles of denaturation (95 °C for 30 s), annealing (55 °C for 30 s), extension (72 °C for 45 s), and a final extension at 72 °C for 10 min. PCR products were pooled in equimolar concentrations of 10 ng μL^{-1}. Paired-end sequencing was performed on an Illumina MiSeq sequencer at Personal Biotechnology

(Shanghai, China). Sequencing of the 18S rRNA gene of one May 2019 sample (T1, replicate D) failed.

We analysed raw sequencing data of 16S rRNA gene and 18S rRNA gene using previously established protocols (Xiong et al. 2021) with some modifications. For 16S rRNA gene analyses, paired-end reads were merged with USEARCH v11 (Edgar 2010) and merged sequences with expected errors > 1.0 or a length < 220 bp were removed. We further identified amplicon sequence variant (ASV) with the UNOISE3 algorithm (Edgar 2016), which simultaneously removed chimeras. We removed the 16S ASVs that contained fewer than 10 reads across all the samples. Finally, the 16S ASV representative sequences were matched against the RDP database (Cole et al. 2014; Wang et al. 2007). To focus on prokaryotic communities, we removed the reads assigned as chloroplast, mitochondria, and eukaryotes. For 18S rRNA gene analyses, merged sequences with a length shorter than 300 bp were removed. Representative eukaryotic ASVs were taxonomically classified against the PR^2 database, which though focussing on protists also covers fungi (Guillou et al. 2013). To focus on fungal and protistan communities, we removed sequencing reads of Rhodophyta, Streptophyta, and Metazoa. Finally the eukaryotic data set was split into a fungal and a protistan one. In certain cases, consensus sequences were further checked, using the Standard Nucleotide BLAST at https://blast.ncbi.nlm.nih.gov/Blast.cgi (Altschul et al. 1990).

Statistical analyses

Statistical analyses were performed in R (R Core Team 2023). Microbial and elemental ratios were natural logarithm-transformed prior to statistical analyses (Isles 2020) and, if parametric, are given as geometric means ± mean 95% confidence intervals as obtained by R package DescTools (Signorell et al. 2022). Other data with continuous response are either given as arithmetic mean ± standard deviation or as median ± median absolute deviation in dependence of the statistical test used. Residuals were checked for normal distribution using Q-Q-plots supplemented by normal curve analysis and Shapiro–Wilk test as provided by *stat.desc* command from pastecs (Grosjean and Ibanez 2018). Similarly, evaluation of residual-versus-fitted plots for checking for homoscedasticity was supplemented by Brown-Forsythe test using *leveneTest* command from car (Fox and Weisberg 2019). In cases requirements for Analysis of Variance (ANOVA) were not met, data were Box-Cox transformed using MASS (Venables and Ripley 2002). One-way ANOVA was performed using car and, if requirements after transformation were still not met, Scheirer-Ray-Hare test was employed using rcompanion (Mangiafico 2023). For considering block effects, this was included as main effect.

In order to account for repeated measures, for potato yield over time, a linear mixed effects model with treatment, year, and block as fixed effects and plot as random effect was employed using nlme (Pinheiro et al. 2023), but the according Box-Cox transformation value λ was obtained from a linear model excluding the random effect. In the case of maize and wheat yields the rotation cycle instead of the year had to be included as fixed effect. In contrast, in the case of long-term soil data, which were obtained after combining the field replicates, sampling time was used for replication and the rotation cycle served as random effect.

Potato quality is expressed as percentage, though data was obtained by counting. Potato quality data over the whole course of the field trial was analysed with generalised linear mixed models and potato quality data of 2019 alone was analysed in addition with generalised linear models, both based on negative binomial distribution using *glmer.nb* from lme4 (Bates et al. 2015) and *glm.nb* from MASS, respectively, together with *Anova* command from car. Dispersion was checked using package DHARMa (Hartig 2022). Depending on the nature of residuals, as post hoc tests either Estimated Marginal Means using emmeans (Lenth 2023) together with the *cld* command from multcomp (Hothorn et al. 2008) or Dunn test using FSA (Ogle et al. 2023) together with the *cldList* command from rcompanion were conducted. All graphics were prepared using ggplot2 (Wickham 2016) with support of scales (Wickham et al. 2023), patchwork (Pedersen 2023) and cowplot (Wilke 2020).

Sampling efficiency of high-throughput sequencing data was estimated using rarefaction curves calculated with iNEXT (Chao et al. 2014; Hsieh et al. 2020) indicating sufficient sampling of prokaryotes, fungi, and protists (Supplementary Fig. S1). Calculations for α- and β-diversity were conducted using the R package vegan (Oksanen et al. 2022). In order to consider different library sizes with smallest ones being 132,649, 5,895, and 36,969 for prokaryotes, fungi, and protists, respectively (for averages see Supplementary Table S6), each ASV table was rarefied randomly 1,000 times and α- and β-diversity were calculated iteratively with finally determining the medians (Hemkemeyer et al. 2019). Observed richness, abundance-based coverage estimator (ACE), exponential Shannon–Wiener index ($e^{H'}$), and Pielou's index (J') were determined using the *estimateR* command. The exponential form of the Shannon-Wiener index was chosen, because it uses numbers of species as unit and is thus easier to interpret (Krebs 1999). Prior to Bray–Curtis dissimilarity determination (*vegdist* command), rarefied counts were square-root transformed to reduce the weight of the most abundant taxa. Differences between treatments were compared by permutational multivariate Analysis of Variance (PERMANOVA, *adonis2* command). Despite highly significant differences, subsequent pairwise

comparison using pairwiseAdonis (Arbizu 2017) could not discern the differing treatments. Homogeneity of variance was checked via permutational analysis of multivariate dispersions (PERMDISP, *betadisper* command) and for visualisation non-metric multidimensional scaling (NMDS, *metaNMDS* command) was employed.

The taxa differing between treatments were identified using edgeR (Robinson et al. 2010). Prokaryotes, fungi, and protists were analysed separately by starting with selecting data using cut-offs of 50, 200, and 100 counts per million in at least four samples, respectively, in accordance with the different orders of magnitude between libraries of the three taxonomic groups (Chen et al. 2015). The different library sizes within each taxonomic group were accounted for by normalisation based on the weighted trimmed mean of log expression ratios "TMM"-method (Robinson and Oshlack 2010). This analysis used the generalised linear model approach (McCarthy et al. 2012) with control of the false discovery rate using the algorithm by Benjamini and Hochberg (1995). Results are shown as heatmaps with displayed taxa being restricted to the most abundant ones.

Results

Long-term crop yields

When winter wheat was the preceding cash crop, planting of oil radish as cover crop in between increased potato yields by 11–16% ($F = 49.7$, $p < 0.001$, Fig. 1a). The different fertilisers employed on oil radish had no further effects. When silage maize preceded potatoes and, thus, oil radish within the crop rotation was positioned prior to maize, potato yields were 8% lower than or similar to the treatment completely omitting the cover crop. In contrast, in both maize-as-pre-crop treatments, maize yields were 4% higher compared to all other treatments ($F = 4.37$, $p = 0.007$, Fig. 1b), while wheat yields did not differ between any cultivation method ($F = 1.51$, $p = 0.230$, Supplementary Fig. S2a). During six crop rotations and ignoring the extreme year 2010, potato yields decreased by 36–44% compared to the first harvest in 2004 depending on the treatment ($F = 533.9$, $p < 0.001$, Fig. 1a).

Long-term potato quality

The reduction of potato quality was highest with maize as pre-crop, contrasting wheat + oil radish as pre-crop with either manure or straw + slurry application, which lowered infections by 63% and 43% with common scab ($X^2 = 26.5$, $p < 0.001$, Fig. 1c) and black scurf ($X^2 = 26.1$, $p < 0.001$, Fig. 1d), respectively. A similar result was observed for dry core with straw + slurry application, leading to 58% lower infections ($X^2 = 29.5$, $p < 0.001$, Fig. 1e). For silver scurf an adverse effect was found in the latter treatment, in which 52% more potatoes were infected than under wheat + oil radish with mineral or straw alone fertilisation ($X^2 = 17.9$, $p = 0.006$, Fig. 1f). The different cultivation methods had no long-term effects on deformations ($X^2 = 9.41$, $p = 0.152$), black dot disease ($X^2 = 6.56$, $p = 0.363$), and wireworm attacks ($X^2 = 4.14$, $p = 0.658$), despite of noticeable occasions in specific years (Supplementary Fig. S2b–d). Like yield, potato quality decreased over time in all rotation systems, i.e. disease incidences increased 3–9-fold for common scab, 16–49-fold for black scurf (except for 2019), 14–65-fold for dry core, and 1.2–3.1-fold for silver scurf (Figs. 1c–f, Supplementary Table S3) and in 2019 wireworms became noticeable.

Long-term soil abiotic characteristics

During the whole trial, wheat + oil radish-pre-crop treatments receiving manure or straw + slurry contained 9–12% and 13–15% higher concentrations of soil organic matter (SOM) and Mg, respectively, than under maize as pre-crop ploughed in spring. Both treatments showed 13–21% more P and 21–27% more K than most other treatments (Supplementary Fig. S3a–d, Table S4). Where oil radish grew in autumn, the content of inorganic N was three-fold lower than where the cover crop was omitted ($F = 9.0$, $p < 0.001$, Fig. S3e). Soil pH did not differ (Fig. S3f, Table S4).

Plant and soil abiotic characteristics in 2019 and 2015

In contrast to the long-term results given above, at potato harvest in 2019, plant quality characteristics hardly differed between treatments (Table S3). Similarly, no treatment effects were observed on soil abiotic factors (Table 2). Soil had 62% water-stable aggregates and a pH of 6.4. Total contents of C and N were 11.7 and 0.95 mg g^{-1}, respectively, and for extractable nutrients like P (65.7 µg g^{-1}) and K (181 µg g^{-1}), see Table 2. Already in February 2015, when sampling took place at another stage of the crop rotation, hardly any differences in abiotic characteristics were observed (Supplementary Table S5, Fig. S4a).

Microbial abundances, activities, and α-diversities in 2019 and 2015

At harvest in 2019, microbial biomass C was unaffected by cultivation treatments, which was also true for microbial derived N, P, and Mn, microbial elemental molar ratios (C:N:P 13:2:1) and the metabolic quotient qCO_2 (Table 3). However, fungal abundances, indicated by ITS1 copies, were

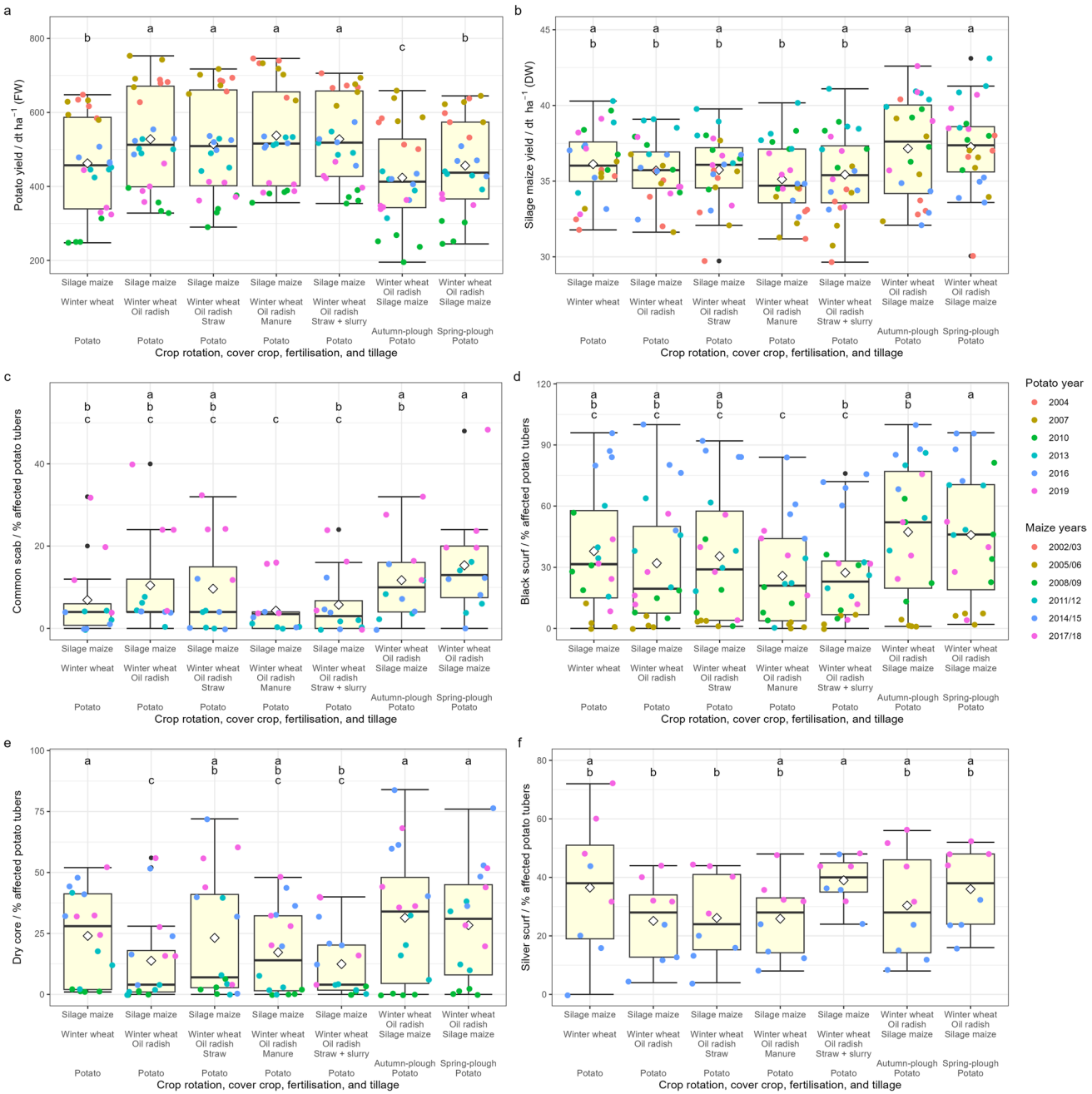

Fig. 1 Yield of potatoes (**a**) and silage maize (**b**) and potato quality indicated by infection with pathogenic *Streptomyces* spp.-induced common scab (**c**), *Rhizoctonia solani*-induced black scurf (**d**) and dry core (**e**), and *Helminthosporium solani*-induced silver scurf (**f**) over several years. Diamonds represent means of four replicates; letters indicate significant differences between treatments ($p < 0.05$)

Table 2 Abiotic soil factors of samples taken at harvest in October 2019 (n = 4)

Response variable	Estimate[a]		Deviation[b]	Test result[c]	p
Water holding capacity / %	49.9	±	1.5	H = 6.08	0.415
Water-stable aggregates / %[d]	61.6	±	9.0	F = 1.50	0.259
pH_{CaCl2}	6.4	±	0.1	F = 0.55	0.763
Total C / mg g^{-1}	11.6	±	1.0	H = 9.41	0.152
Total N / mg g^{-1}	0.95	±	0.08	F = 1.61	0.201
Total S / mg g^{-1}	0.12	±	0.02	H = 6.51	0.368
Extractable C / µg g^{-1}	59.6	±	9.0	H = 7.84	0.250
Extractable N / µg g^{-1}	16.7	±	4.8	F = 1.25	0.328
Extractable P / µg g^{-1}	65.7	±	12.2	F = 1.31	0.301
Extractable S / µg g^{-1}	29.0	±	12.2	F = 1.56	0.216
Extractable K / µg g^{-1}	164.1	±	31.7	H = 3.28	0.773
Extractable Ca / µg g^{-1}	987	±	150	H = 3.33	0.767
Extractable Mg / µg g^{-1}	99.1	±	22.2	H = 6.01	0.422
Extractable Mn / µg g^{-1}	0.024	±	0.000	H = 5.39	0.495
Extractable Si / µg g^{-1}	31.4	±	21.6	F = 0.13	0.990

[a]Mean or median in dependence of the statistical test used

[b]Standard deviation or median absolute deviation

[c]ANOVA (F) or Scheirer-Ray-Hare test (H)

[d]n = 3 (only blocks B–D)

Table 3 Biotic soil factors of samples taken at harvest in October and May 2019 (n = 4)

Response variable	Estimate[a]		Deviation[b]	Test result[c]	p
October 2019					
Microbial biomass C / µg g^{-1}	123.4	±	24.3	F = 1.99	0.121
Microbial biomass N / µg g^{-1}	25.0	±	5.2	F = 1.51	0.231
Microbial biomass P / µg g^{-1}	27.7	±	26.3	H = 5.97	0.427
Microbial biomass C:N (mol/mol)	5.7	±	0.4	F = 1.56	0.215
Microbial biomass C:P (mol/mol)	10.9	±	6.5	H = 3.56	0.736
Microbial biomass N:P (mol/mol)	2.7	±	0.9	F = 1.43	0.323
Microbial biomass Mn / µg g^{-1}	0.33	±	0.17	F = 1.59	0.205
Microbial biomass C:Mn (mol/mol)	1,902	±	910	H = 9.11	0.167
Basal respiration / CO_2-C µg g^{-1} d^{-1}	5.54	±	2.55	F = 0.67	0.675
qCO_2 / µg CO_2-C mg^{-1} MBC d^{-1}	48.2	±	30.9	F = 0.31	0.921
Net N mineralisation / N_{min}-N µg g^{-1} d^{-1}	0.71	±	0.51	F = 1.46	0.248
Bacterial 16S rRNA gene copies g^{-1}	$1.43 \cdot 10^{10}$	±	$0.24 \cdot 10^{10}$	H = 6.72	0.347
Archaeal 16S rRNA gene copies g^{-1}	$2.98 \cdot 10^{8}$	±	$0.40 \cdot 10^{8}$	F = 0.69	0.661
Bacteria:archaea ratio	45.9	±	3.1	F = 1.77	0.162
Bacteria:fungi ratio	70.3	±	4.0	F = 2.14	0.098
Archaea:fungi ratio	1.5	±	0.1	F = 1.59	0.211
May 2019					
Bacterial 16S rRNA gene copies g^{-1}	$1.37 \cdot 10^{10}$	±	$0.23 \cdot 10^{10}$	F = 0.55	0.763
Archaeal 16S rRNA gene copies g^{-1}	$2.57 \cdot 10^{8}$	±	$0.44 \cdot 10^{8}$	F = 1.34	0.292
Bacteria:archaea ratio	53.4	±	2.4	F = 1.66	0.188

[a]Mean (geometric mean for ratios) or median in dependence of the statistical test used

[b]Standard deviation, median absolute deviation, or, for geometric mean, mean 95% confidence interval

[c]ANOVA (F) or Scheirer-Ray-Hare test (H)

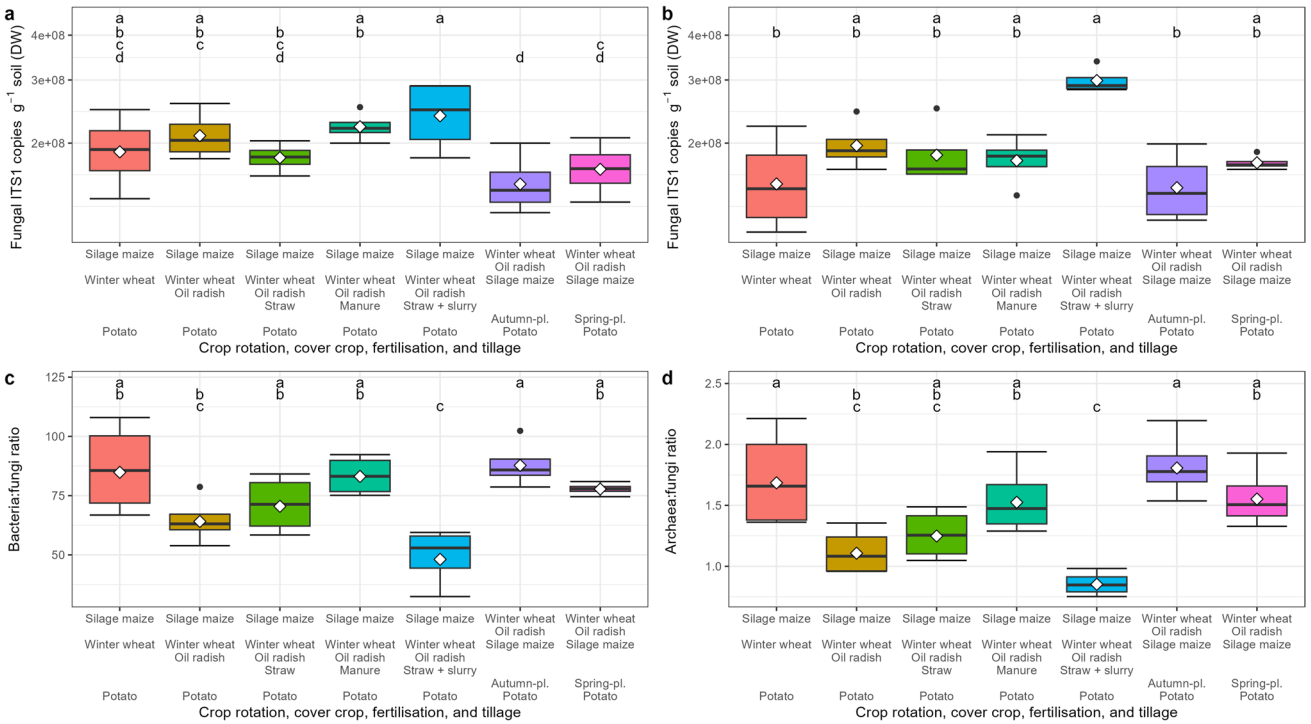

Fig. 2 Fungal abundance in samples of October 2019 (**a**) and May 2019 (**b**) and fungal ratios in May 2019 with bacteria (**c**) and archaea (**d**). Diamonds represent means of four replicates; letters indicate significant differences between treatments ($p < 0.05$); statistical results of ANOVA (F) and Scheirer-Ray-Hare (H) tests were a: $F = 7.05$, $p < 0.001$; b: $H = 12.94$, $p = 0.044$; c: $F = 9.02$, $p < 0.001$; d: $F = 12.29$, $p < 0.001$

42% more abundant where wheat + oil radish grew before potatoes with manure or straw + slurry application than in treatments with maize as pre-crop ($F = 7.05$, $p < 0.001$, Fig. 2a). In contrast, bacterial and archaeal 16S rRNA gene copies g^{-1} soil as well as microbial ratios did not respond to treatments (Table 3, molecular bacteria:archaea:fungi ratio 70:2:1). Observed richness of prokaryotic, fungal, and protistan amplicon sequence variants (ASVs) as well as estimated richness, diversity index, and, except for protists, evenness were also unaffected by cultivation treatments (Supplementary Table S6, Fig. S4b). With few exceptions, these patterns were in line with findings from sampling in 2015 (Table S5, Fig. S4c) and at seeding time (Table 3, Figs. 2b–d, Supplementary Table S6, Fig. S4d).

Microbial β-diversity and taxa differing between cultivation treatments in 2019

Among prokaryotic communities, two groups of treatments clustered most strongly away from each other at harvest: one group consisted of those treatments with wheat + oil radish as pre-crop and manure or straw + slurry application, while the other group contained the treatments with maize as pre-crop ($F = 1.16$, $p = 0.009$, Fig. 3a). Clustering between different pre-crops was even more pronounced for fungi ($F = 1.63$, $p = 0.001$, Fig. 3b) and protists ($F = 1.46$, $p = 0.001$, Fig. 3c). Where wheat was the pre-crop, fungi were further separated by straw + slurry application. At seeding, mentioned clusters in all three microbial groups were even stronger separated from each other (Fig. 4). An overview of the microbial community compositions is given in Supplementary Results S1 and Figs. S5–S7.

Analysis of ASVs differing between cultivation methods at harvest showed that 0.5% of the prokaryotic ones making up to about 3% of the sequences in the libraries derived from treatments with wheat + oil radish as pre-crops under manure or straw + slurry application, while they accounted for 1.3–1.6% of the sequences in the other treatments. Strongest drivers of this pattern were Firmicutes (2.0–2.4%) with the classes Bacilli, Clostridia, and Erysipelotrichia (Fig. 5, Supplementary Table S7). Both maize-as-pre-crop treatments shared a *Streptomyces* ASV (Zotu569, Actinobacteria, 0.06%), which according to BLAST was not related to common scab-inducing species.

Among fungi, 8% of ASVs differed between treatments, of which most of them could only be classified to subphylum or class level (Fig. 6, Supplementary Table S8). While in most treatments they accounted for 3–10% of the sequences, under straw + slurry application they reached 38%. This treatment fostered several ASVs comprising *Mortierella*/

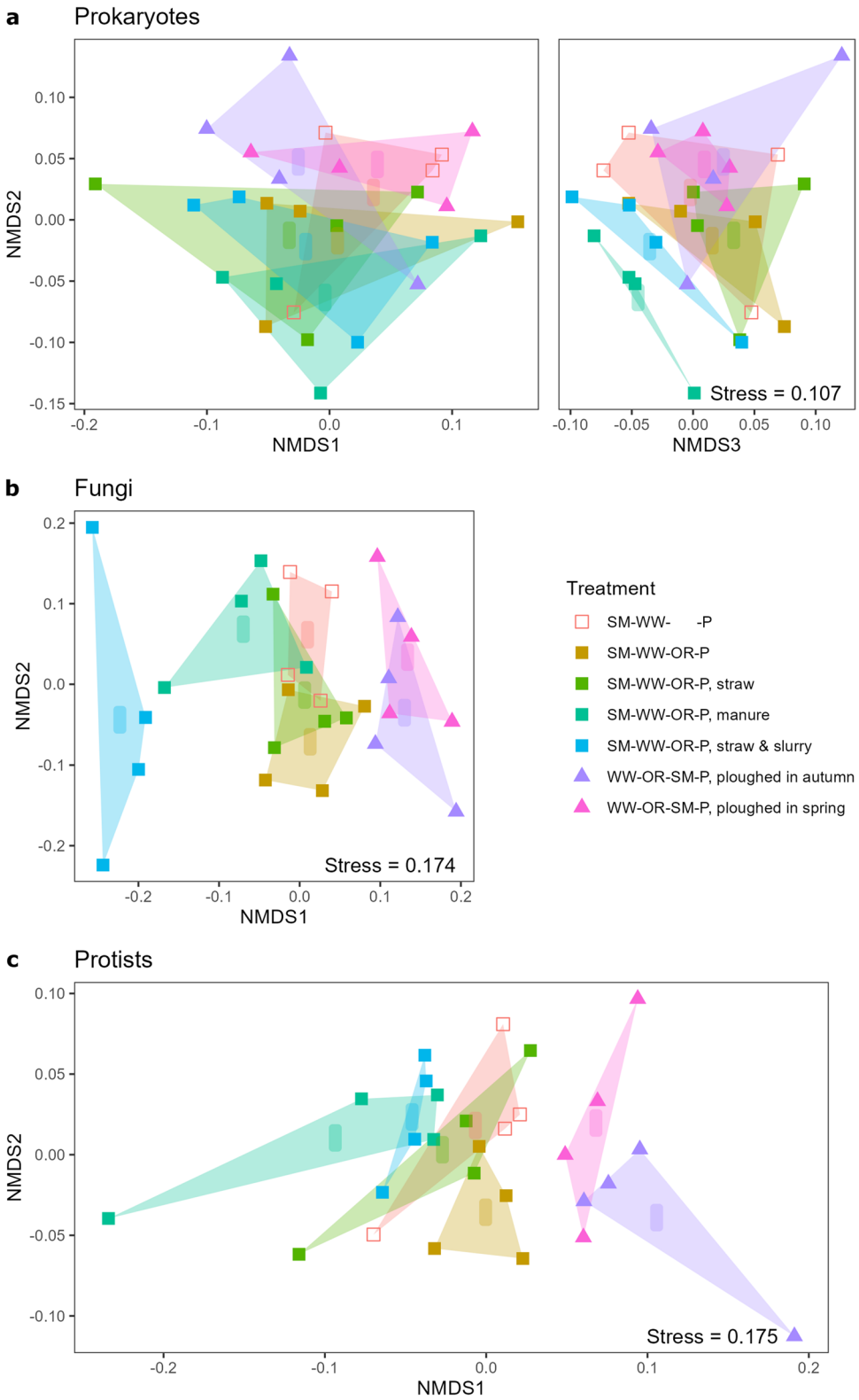

Fig. 3 Non-metric multidimensional scaling plots of samples taken at harvest in October 2019 for treatments differing in the crop rotations of silage maize (SM), winter wheat (WW), oil radish (OR), and potatoes (P). Upright rounded rectangles indicate the position of the centroids

Mucoromycotina (28%) with next relatives all belonging to Mortierellaceae according to BLAST (Mucoromycota) and Pezizomycotina/ Pezizomycetes (Ascomycota, 9%) with the majority being related to *Ascodesmis*. Both maize-as-pre-crop treatments shared *Acremonium persicinum* (Ascomycota, 0.3%).

Also, the 3% protistan ASVs differing were most abundant in the treatment with straw + slurry application with

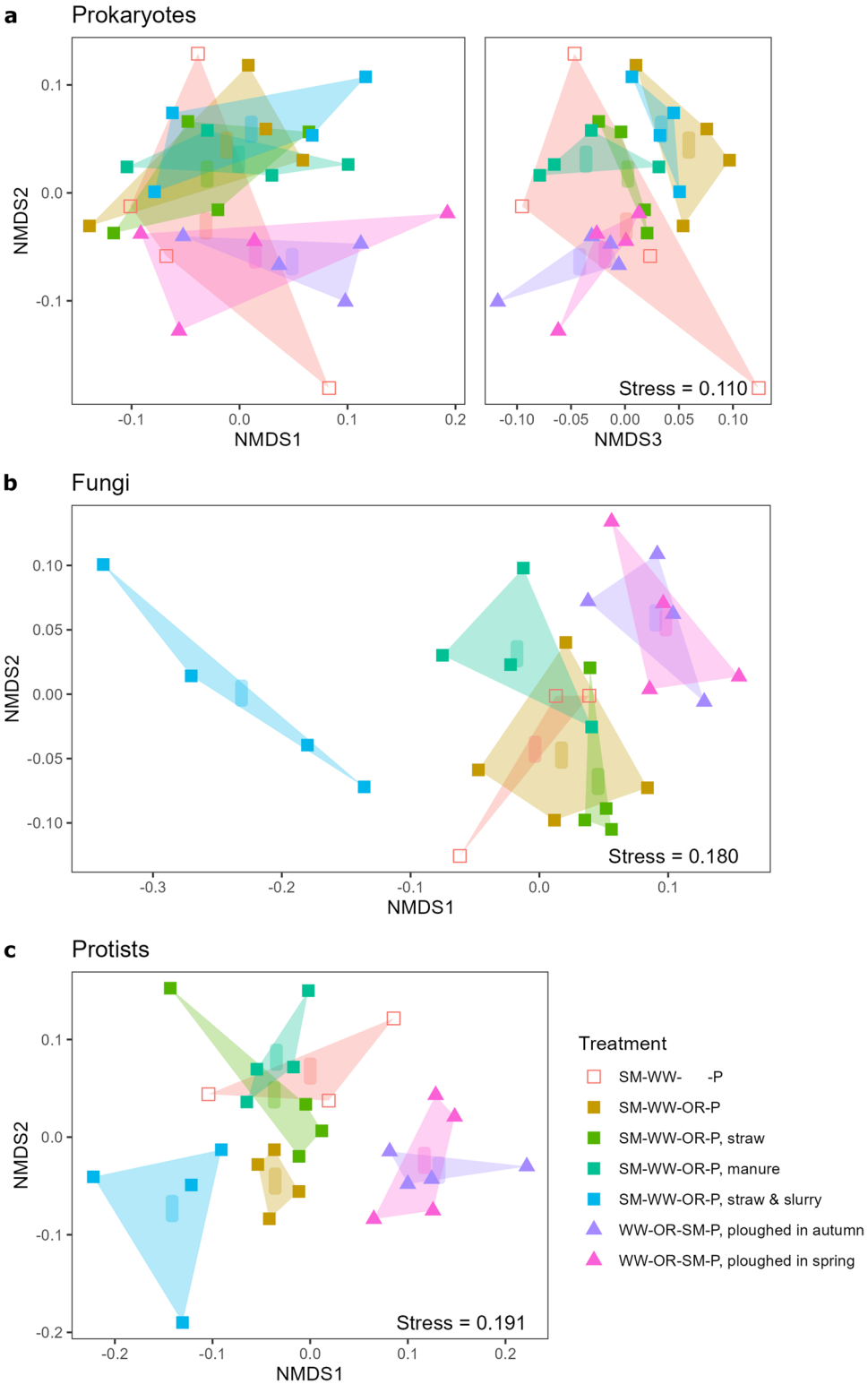

Fig. 4 Non-metric multidimensional scaling plots of samples taken at seeding in May 2019 for treatments differing in the crop rotations of silage maize (SM), winter wheat (WW), oil radish (OR), and potatoes (P); upright rounded rectangles indicate the position of the centroids. Results of PERMANOVA were a: F = 1.232, p = 0.001; b: F = 2.006, p = 0.001; c: F = 1.574, p = 0.001

18% of the sequences, while in the other treatments they ranged 11–14%. Here a *Neoheteromita*-ASV (Cercozoa, 3.2%) was 2.3-fold more abundant (Fig. 7, Supplementary Table S9). However, in both the straw + slurry and the manured treatment ASVs of Lobosa, especially *Copromyxa*, and Ochrophyta were 62% and two-fold, respectively, more abundant than in other treatments. Where maize was the pre-crop, Chlorophyta-ASVs were 64% more abundant. For more differing ASVs, see Supplementary Results S2.

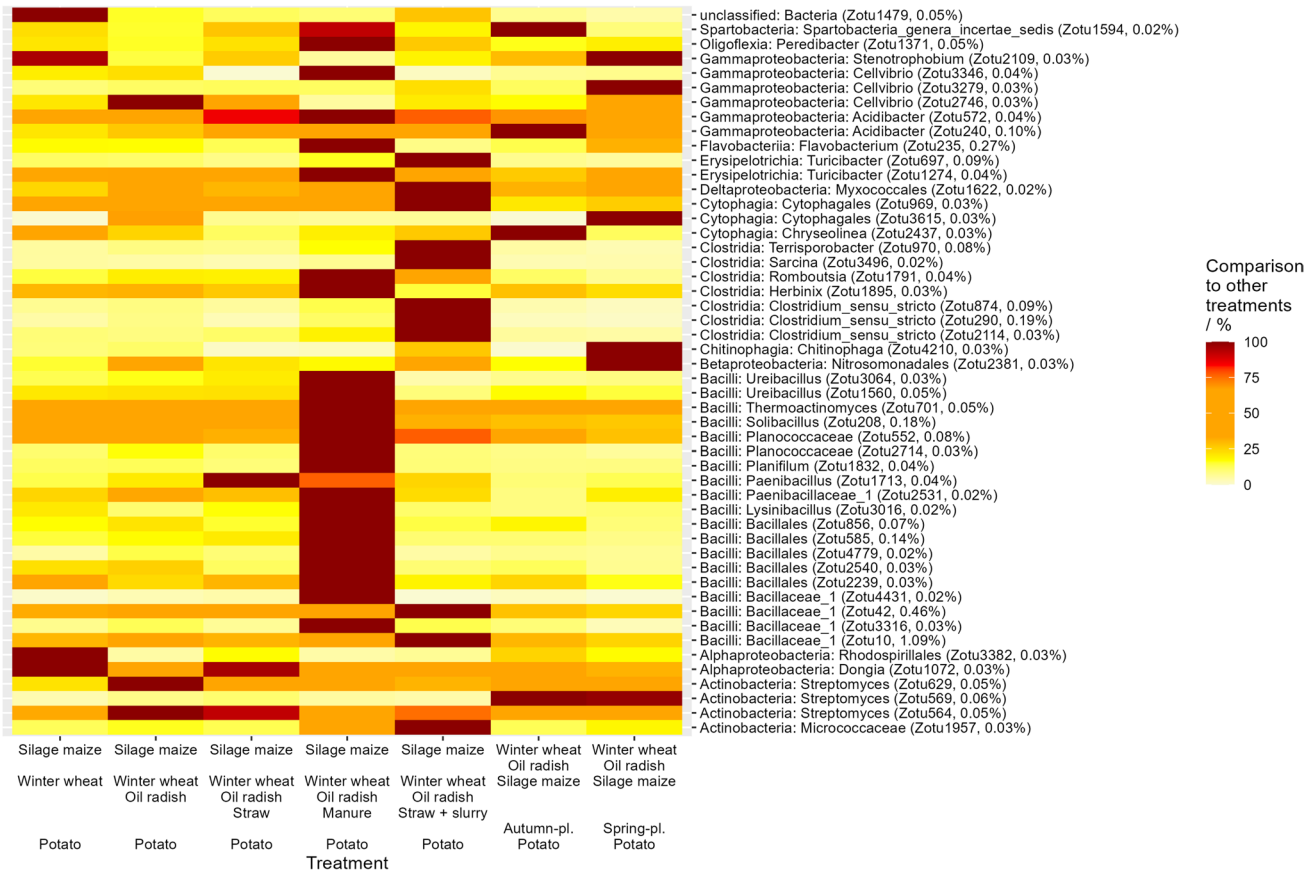

Fig. 5 Top 50 abundant prokaryotic ASVs significantly differing between potato cultivation treatments at harvest in October 2019. ASVs are given as class for purpose of ordering, the lowest taxonomic rank to which an ASV was identified, ASV number (Zotu), and the mean percentage of ASV sequences to all sequences in the treatment containing the highest abundance of the given ASV. For statistical results see Supplementary Table S7

When calculating β-diversity across seeding and harvest data, NMDS (data not shown) and PERMANOVA indicated a strong effect of sampling time for composition of prokaryotic ($F = 3.50$, $p = 0.001$), fungal ($F = 4.66$, $p = 0.001$), and protistan communities ($F = 8.22$, $p = 0.001$) without significant interaction of treatment and sampling time ($p \geq 0.478$). Percentages of differing prokaryotic, fungal, and protistan ASVs and their contribution to respective libraries were always much larger at seeding with 0.8% (library contribution 3.0–6.9%), 14% (9.2–45.7%), and 4.7% (15.9–25.4%), respectively, than at harvest. Also, the 50 most abundant differing ASVs differed between both sampling times (*cf.* Figure 5–7 and Supplementary Figs. S8–S10, Tables S10–12). However, several ASVs showing differences at harvest already displayed these differences at seeding time like several ASVs of the Firmicutes (e.g. Zotu10, 290, 697), *Streptomyces* (Zotu629, 569), Mucoromycotina (Zotu310, 12, 128), Pezizomycetes (Zotu87, 1791), *A. persicinum* (Zotu1279), Plasmodiophorida (Zotu16), *Neoheteromita* (Zotu7), Prasiolales (Zotu167), Cercozoa (Zotu43), and Sandonidae (Zotu100).

Discussion

Potato yield and the role of oil radish as cover crop

Combinations of wheat as pre-cash crop and subsequent oil radish led to highest potato yields in the current study. The different cultivation methods led to differences in the long-term soil characteristics (SOM, P, K, Mg), but their patterns did not match with yield, thus, there is no correlation between yield and concentration of these nutrients. For samplings in 2015 and 2019, there were hardly any differences in the nutritional status of soils, i.e. hypothesis 2 partly rejected for yield. Also, the differences in microbial abundances, activities, and α-diversities, i.e. hypotheses 3–5 must be rejected for yield. The same is true for microbial β-diversity patterns. Thus, yield effects can be related to the presence of the cover crop or its position within the rotation.

The lower yield in the treatment omitting the cover crop could be connected to the number of fertilisation occasions, which was one less per cycle. Furthermore, soil inorganic N content was lower after oil radish cropping (T2–T8) than

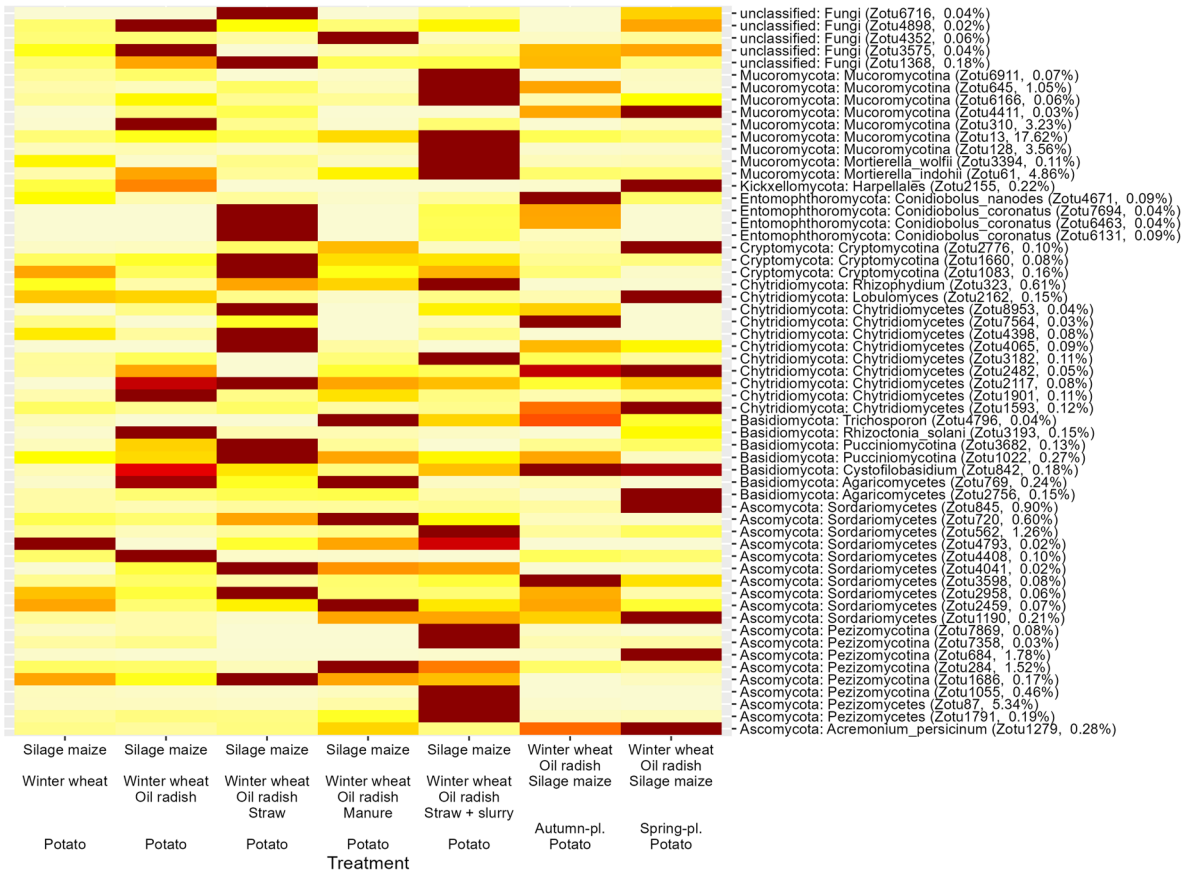

Fig. 6 Fungal ASVs significantly differing between potato cultivation treatments at harvest in October 2019. ASVs are given as phylum for purpose of ordering, the lowest taxonomic rank to which an ASV was identified, ASV number (Zotu), and the mean percentage of ASV sequences to all sequences in the treatment containing the highest abundance of the given ASV. For statistical results see Supplementary Table S8

under fallow after wheat (T1), despite omitted fertilisation, indicating N uptake by the cover crop. Nutrients taken up remain on the field and get released upon the decay of cover crops (Kaspar and Singer 2011; Maltais-Landry and Frossard 2015). On the one hand, the cover crop with its accompanying fertilisation represents a direct input of additional nutrients and, on the other hand, it prevents the loss of already available nutrients by leaching, e.g. nitrate, or gaseous emission, e.g. nitrous oxide. Accordingly, potatoes of the treatment omitting oil radish missed out on further nutrition. Thus, hypothesis 2 is rejected for yield, as the according nutrients were not stored freely in the soil but in the cover crop.

When maize was the pre-crop of potatoes, oil radish was grown one year earlier and, thus, directly before maize. Therefore, it was maize, which benefitted from the cover crop as shown by higher maize yields in these treatments as also observed by Kaye and Quemada (2017). In contrast, wheat always grew before the cover crop and did not show direct yield benefits. Consequently, the cover crop directly grown before potatoes causes the difference in yield, rather than direct impacts by wheat or maize as pre-crops. Benefits in potato yield by oil radish have also been reported by Hamzaev et al. (2007). As silage maize gets harvested later than winter wheat, there is not enough time for subsequent growth of cover crops for sufficient N uptake (Kivelitz 2017; Komainda et al. 2016). Thus, maize as pre-crop has an indirect effect on potato yield by precluding cover crops with function as catch crops, i.e. hypothesis 1 confirmed for yield.

Potato quality and microbial communities

Highest long-term potato qualities regarding lowest infection with common scab, black scurf, and dry core were found where wheat + oil radish was the pre-crop under application of manure or straw + slurry, contrasting both treatments with maize as pre-crop. The high qualities were accompanied by highest long-term concentrations of extractable P and K, whereas both contrasting treatments only partially matched the long-term patterns of SOM and extractable Mg, i.e. hypothesis 2 partly confirmed, partly rejected for quality depending on nutrient. Higher nutritional supply

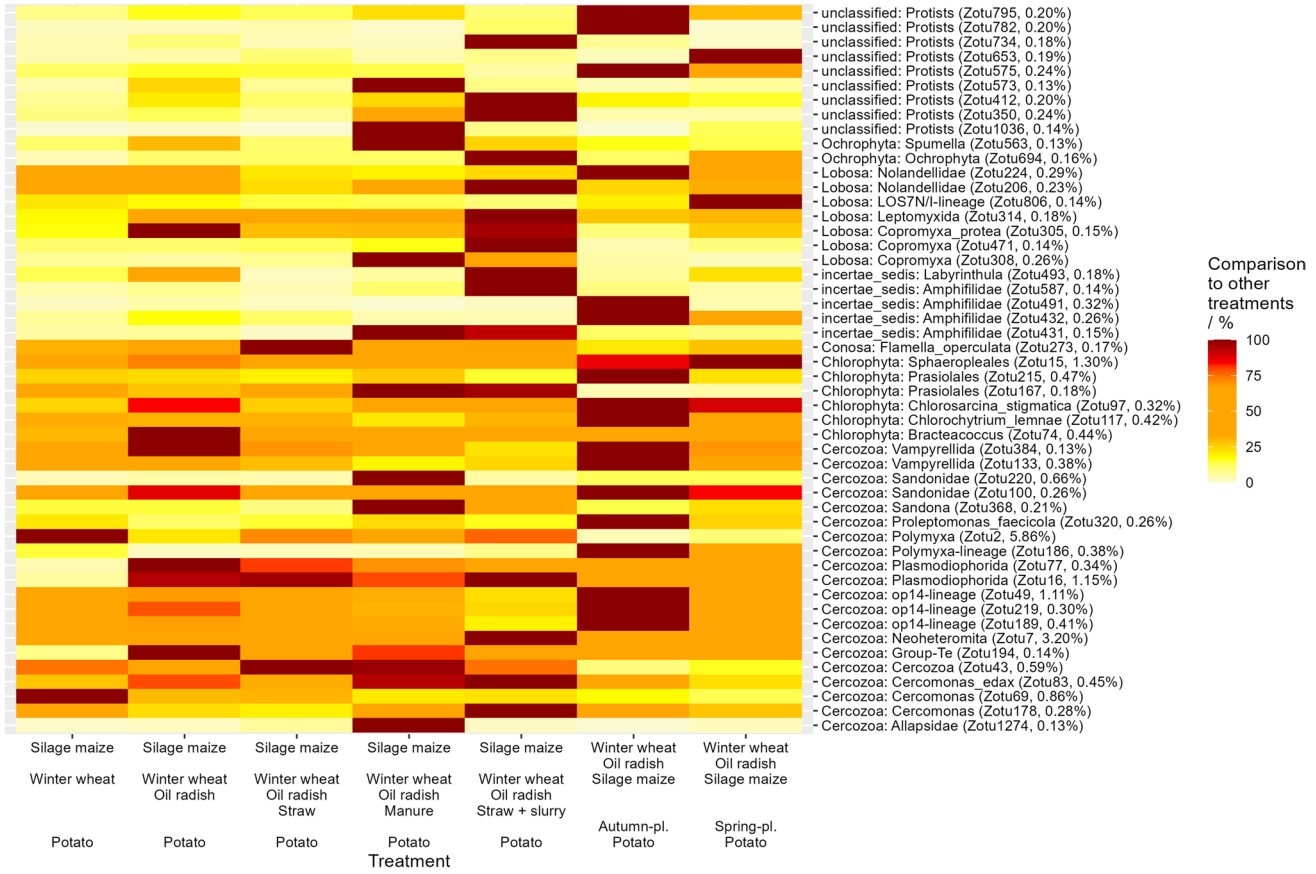

Fig. 7 Top 50 abundant protistan ASVs significantly differing between potato cultivation treatments at harvest in October 2019. ASVs are given on a high rank, e.g. phylum, for purpose of ordering, the lowest taxonomic rank to which an ASV was identified, ASV number (Zotu), and the mean percentage of ASV sequences to all sequences in the treatment containing the highest abundance of the given ASV. For statistical results see Supplementary Table S9

can strengthen the resistance of plants against pathogens (Chandrashekara et al. 2012). In 2019, when there were hardly any differences in potato qualities, there were no differences in soil abiotic characteristics detectable. Similar to abiotic factors in 2015, this came along with missing differences in microbial abundances, activity, and α-diversity, i.e. hypotheses 4–5 rejected for quality. Suppressive soils generally contain higher values in these microbial properties than non-suppressive soils (Chandrashekara et al. 2012; Jayaraman et al. 2021).

However, fungal abundance in 2019 was an exception, indeed matching the long-term quality patterns with positive correlation, i.e. hypothesis 3 mainly rejected for quality except in case of fungi. A similar result for fungi was not observed for the 2015 samples, when the field was in another stage of the crop rotation and two characteristic treatments (T6 and T8) were not included in qPCR analysis. However, the 2019 patterns of β-diversity of prokaryotes, fungi, and protists matched the long-term quality patterns. The different cultivation methods, i.e. pre-crop (wheat vs. maize including differences in tillage intensity and pesticide application) and different fertilisation types led to changes in the microbial community compositions. For instance, regarding the different types of fertilisation associated with the cover crop, a nutrient that is supplied in mineral form can address other microbial species than one supplied in organic form (Lilleskov et al. 2002). The match of disease suppression in treatments between 2004 and 2016 with fungal abundance and microbial β-diversity in 2019 could be related to a microbial legacy as discussed below. In contrast, silver scurf showed a different pattern of treatments in regard to lowest or highest percentages of infected tubers, whereas black dot disease was unaffected by the different cultivation methods. Accordingly, confirmation or rejection of hypotheses in regard to quality depends on kind of disease.

The omission of the cover crop leading to a fallow period had no obvious effect, as this treatment had medium disease incidence. Microbial communities clustered between both contrasting groups, together with the other wheat-as-pre-crop treatments without animal-derived fertiliser. In contrast to meta-analytical findings (Kim et al. 2020), cover crop inclusion compared to omission had no significant effects on

microbial abundance, activity, or diversity in our study, i.e. hypothesis 1 cannot be related to hypotheses 3–5 for quality. For fungal communities in intensive potato production, it has been shown that, despite a three-year crop rotation, they will shift to a potato adopted community (Manici and Caputo 2009).

Comparison of differing ASVs between seeding and harvest

At harvest, in all treatments potatoes were grown, while at seeding time the recent rhizospheric legacy derived from three different preceding crops, i.e. oil radish cover crop, maize, or wheat still prevailed to an unknown extent. During potato growth the numbers and sums of contributions of differing ASVs were reduced along with the reduced plant diversity (from three pre-crops to one main crop), revealing the importance of considering the pre-crop legacy for soil microbial investigations. Nevertheless, several ASVs showing a specific association with a certain treatment were found at both time points. Remaining relic DNA cannot be ruled out (Levy-Booth et al. 2007) and, as many of the ASVs were classified as spore formers or showing other kinds of persistence (Bulman and Neuhauser 2017; Howe et al. 2009; Ottow 2011) like dormancy (Joergensen and Wichern 2018), inactive cells might have contributed to the observed patterns. However, several of these ASVs include potential antagonists and plant growth promoting rhizobacteria, which could have played a role in influencing the quality of potatoes. As no microbiological investigations were done at the beginning of the trial or throughout the 19 year trial, it can only be speculated whether the same or similar taxa were already involved in potato quality in the past.

Microbial members potentially involved in potato quality

Firmicutes, which drove the difference under manure and (straw +)slurry application, process fresh and simple substrates with some taxa even being specialised on urinary sources and, after food sources decline, their cells can survive in the form of spores (Ottow 2011). The effect on the bacterial community composition in the manure and slurry treatments mainly derives from fostering members of the autochthonous community rather than from establishment of allochthonous livestock gut-derived bacteria (Chu et al. 2007; Sun et al. 2015). *Bacillus* species/isolates are commonly found among genera suppressing diseases (Agrios 2005), including common scab (Braun et al. 2017), *R. solani*-induced diseases (Kiptoo et al. 2021), and silver scurf (Avis et al. 2010). Several *Bacillus* species/isolates are often considered as plant growth promoting rhizobacteria for potatoes (Calvo et al. 2010; Ekin 2019; Ghyselinck et al. 2013; Hanif et al. 2015). *Paenibacillus* is a known antagonist of *R. solani* (Brewer and Larkin 2005), while *Lysinibacillus*, *Clostridium* sensu stricto, and *Turicibacter* were enriched in the geocaulosphere soil, i.e. the soil surrounding the tuber, associated with reduced common scab occurrence (Shi et al. 2019).

The finding of *Ascodesmis* among the Pezizomycotina/Pezizomycetes in straw + slurry is not surprising, as this genus, though also found in soil, is strictly coprophilous (Kristiansen 2011; van Brummelen 1981) and also some members of Mortierellaceae have been isolated from dung (Domsch et al. 2007). The latter family is often reported to degrade chitin (Domsch et al. 2007) and one member of *Mortierella* was found being antagonistic against common scab-inducing *Streptomyces* spp. (Tagawa et al. 2010). Under potato monocultures, which become prone to pathogens over time, abundances of Mortierellales were decreased (Liu et al. 2014).

Among protistan Lobosa, several mycophagous species also feed on spores (Geisen et al. 2016) and could thus be potential predators of phytopathogenic fungi. Especially the appearance of *Copromyxa* spp. in the manure/straw + slurry treatments is not surprising as these are coprophilic organisms which employ partly a "slime mould" life style (Brown et al. 2011). Thus, the treatments leading to highest potato quality harboured more beneficial prokaryotic, fungal, and protistan taxa in terms of plant growth promotion and disease suppression, i.e. confirming hypothesis 6 in regard to potato quality.

In the treatments with maize as pre-crop, the time point of ploughing led to different driving ASVs. However, some ASVs were common amongst both. The genus *Acremonium* was increased in potato monocultures, which became prone to pathogens over time (Liu et al. 2014). As the *Streptomyces* ASVs could not be identified further, their role remains unclear. Many non-pathogenic *Streptomyces* species are also common PGPR (Bhat et al. 2022) and suppressors of diseases (Agrios 2005), including common scab (Braun et al. 2017) and silver scurf (Avis et al. 2010). Despite incidences of infections increased over time, ASVs of phytopathogens were hardly detected in 2019 samples as discussed in Supplementary Discussion S1.

Limitations of the study design

The design of the field trial was based on regional potato cultivation and crop rotation practices and, thus, had not a factorial design. Accordingly, some factors cannot be discerned. Tillage intensity and pest management differed not within, but between the treatments having wheat (T1–T6) and maize (T7–T8) as pre-crop and might had influenced the outcomes, which in the following are ascribed to the both pre-crop treatment groups. Furthermore, when in 2019 the samplings for microbial community analyses were completed, potato qualities showed no significant differences for the first time.

Therefore, this study discusses microbial data in the context of long-term agronomic results rather than just focussing on the concerted sampling year 2019. However, microbial community abundances, activities, and diversities were only analysed in 2019 when potatoes were present and in the previous crop rotation cycle in 2015 with no potatoes being present. These communities represent the legacy of five to six crop rotation cycles under different treatments and the contemporary conditions at the sampling times, which we cannot disentangle, as accompanying samplings had not been done during the earlier cycles. Nevertheless, we still believe that the major impact arises from the direct predecessor and results should mostly represent the legacy left by the crop grown directly before.

The results discussed above are in particular representative for the last crop rotation cycles, however, they likely show the imprint of the differences in crop rotation and management. It would be of high value if future long-term trials combine agronomic and microbial measurements constantly to also document potential temporal changes in the microbiome with potential impact on potato yield and quality effects. However, this is hardly the case in the current literature, as either microbiologists or plant scientists with a focus on agronomy initiate investigations. We therefore have a strong plea for more truly interdisciplinary research with relevance for agricultural practise.

Conclusions

Six three-year crop rotation cycles of cultivation methods for potatoes, differing in pre-crop/tillage intensity, cover crop inclusion, and type of fertilisation led to clear impacts on yield and quality. On the one hand, the long-term differences in potato quality regarding common scab and *R. solani*-induced diseases were reflected by the community compositions of prokaryotes, fungi, and protists in 2019. This contrasted between wheat + oil radish under manure or straw + slurry application and the treatments with preceding maize. Several ASVs found in the first group of treatments correlated with higher potato qualities potentially caused by plant growth promoting rhizobacteria or antagonists of phytopathogens. Whether these taxa were already earlier involved in improved potato quality remains speculative in the current long-term trial. This first group of treatments also contained highest fungal abundances and long-term soil P and K. On the other hand, potato yield was reflected by the presence or positioning of the cover crop within the rotation, as the crop directly succeeding oil radish received its benefits and produced higher yields. This study demonstrates that a cover crop preceding potatoes and fertilisation with manure or straw + slurry can be recommended for obtaining high yields and qualities. Future agronomic long-term trials should consider microbiological analyses right from the beginning. Such a combined monitoring could also take dynamics due to temporal variability into account enabling the disentanglement of short- and long-term effects of the interplay between agronomic management, crop species and soil microbial communities.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00374-024-01813-0.

Acknowledgements We like to thank all the technicians of the Agricultural Chamber involved in the field trial as well as the academic technician and the student assistants for their excellent work and support in the field and the labs. Liu Chen kindly uploaded the sequences. We also acknowledge the constructive feedback of the editor and the anonymous reviewers.

Author contributions Conceptualisation: Clara Berendonk (field trial), Stefan Geisen, Stefanie Heinze, Florian Wichern; Data curation: Clara Berendonk, Wu Xiong; Formal analysis: Michael Hemkemeyer, Sanja A. Schwalb; Funding acquisition: Clara Berendonk (field trial), Florian Wichern; Investigation: Michael Hemkemeyer, Sanja A. Schwalb, Clara Berendonk, Peter Lövenich, Wu Xiong; Methodology: Sanja A. Schwalb; Project administration: Clara Berendonk (field trial), Peter Lövenich (field trial), Florian Wichern; Resources: Rong Li; Supervision: Rainer Georg Joergensen, Florian Wichern; Validation: Stefan Geisen; Visualisation: Michael Hemkemeyer, Sanja A. Schwalb; Writing – Original Draft: Michael Hemkemeyer; Writing – Review & Editing: all authors.

Funding Open Access funding enabled and organized by Projekt DEAL. The field trial and the long-term analyses were funded by the Agricultural Chamber of North Rhine-Westphalia. The academic analyses were funded by the Ministry of [Climate Action,] Environment, Agriculture, Nature Conservation and Consumer Protection of the State North Rhine-Westphalia (project EffiZwisch) and the Ministry of Culture and Science of the State North Rhine-Westphalia in association with Project Management Jülich (grant number 005–1703-0025, project Soil ionoMICS). Open access publication was enabled by project DEAL.

Data availability The long-term agronomic and soil data are available at request (clara.berendonk@gmx.de). The single time point soil and microbial data obtained in 2019 and 2015 are provided as Supplementary Data S1 and S2, respectively. The raw sequences are available from the Genome Sequence Archive (https://ngdc.cncb.ac.cn/gsa) under accession number CRA010961 with the sample description consisting of treatment number, block, and indicator for sampling time, i.e. S for seeding and H for harvest, to be found under BioProject number PRJCA016846.

Declarations

Competing interests The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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