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Nitrifier denitrification potentially dominates N_2O production in a sandy soil – results from different fertilization and irrigation regimes in potato cropping in Germany

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Abstract. Spatial and temporal distribution of water and nitrogen supply affects soil-borne nitrous oxide (N_2O) emissions. In this study, the effects of different irrigation technologies (no irrigation, sprinkler irrigation and drip irrigation) and nitrogen (N) application types (broadcasted and dissolved in irrigation water) on N_2O emissions and the potentially underlying, genetically determined microbial processes were investigated over an entire season in potato cropping. N_2O fluxes were highest during the first half of the season and mostly affected by the applied water volume rather than the N application types. The comparison of the different water application types revealed that nitrifier denitrification might potentially be the dominant source of N_2O emissions, especially under sprinkler irrigation. The type of N fertilizer supply, broadcasted application or dissolved in irrigation water, showed only minor differences in the potential microbial community functionality. N_2O production in both treatments was most likely also dominated by nitrifier denitrification, while the process of denitrification might be feasible too. Even though the current agronomic management measures generally meet the crop demand of water and N, it might be recommendable to adapt the time of application considering that potatoes mainly require N at later growth stages which could also reduce N_2O emissions at the same time.

1 Introduction

Nitrous oxide (N_2O) is one of the most important greenhouse gases (GHG) with a global warming potential 273-times higher than carbon dioxide (IPCC, 2021). As the atmospheric N_2O concentration has risen by 23 % compared to pre-industrial times (IPCC, 2021), there is an urgent need to mitigate N_2O emissions being mainly caused by the agricultural sector (Jia et al., 2019; Tian et al., 2020; Kuang et al., 2021; Liang and Robertson, 2021).

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It is assumed that by 2050 agricultural crop productivity needs to be increased by 70-100 % to maintain the estimated world population of nine billion people (Wang et al., 2021). Higher agricultural production is often accompanied by increasing application of mineral fertilizer, in particular nitrogen (N) (Tian et al., 2020; Wang et al., 2021; Menegat et al., 2022). Current agricultural systems are characterized by a low nitrogen use efficiency (NUE), resulting inter alia in the loss of large amounts of actually available N through nitrate leaching and/or the generation of N_2O (Wang et al., 2020; Wang et al., 2021; Menegat et al., 2022). Additionally, the progressive climate change intensifies the pressure on the agricultural sector due to extended periods of drought and changing precipitation patterns (IPCC, 2019). Therefore, irrigation becomes more important to guarantee an efficient agricultural crop production (Drastig et al., 2016; Kuang et al., 2021). However, irrigation in general increases the soil water content and hence anaerobic soil conditions resulting in higher N_2O emissions (Butterbach-Bahl et al., 2013; Hu et al., 2015; Kuang et al., 2021). Moreover, different irrigation types (e.g., sprinkler or drip irrigation) are supposed to affect the amount of emitted N_2O, with lower emission rates for drip irrigated systems (Kuang et al., 2021). The combined application of dissolved N in irrigation water and its multiple applications in smaller doses (so-called fertigation) is assumed to minimize N_2O emissions due to reduced availability of N for microbial-mediated processes (e.g. Tian et al., 2017; Zhang et al., 2019; Kuang et al., 2021).

In order to guarantee a sustainable agricultural production with high crop yields and low detrimental environmental impacts, it is not only essential to assess the effects of agronomic management measures on N_2O flux rates and hence N_2O emissions, but also to better understand the underlying microbial-mediated mechanisms. Soil microbial communities are influenced by soil physical and chemical factors such as soil type/structure, soil moisture, oxygen availability, temperature, pH value, availability of the reactive N compounds (e.g., ammonium (NH_4^+) and nitrate (NO_3^-)) as well as root exudates segregated by the cultivated crop (Butterbach-Bahl et al., 2013; Hu et al., 2015; el Zahar Haichar et al., 2016; Kumar et al., 2020).

Within the N cycle, N_2O is primarily caused by the denitrification pathway (NO_3^- to N_2O/N_2), or as a "by-product" of nitrification (NH_4^+ to NO_3^-) including nitrifier denitrification (NH_4^+ via NH_2OH and NO to N_2O), or dissimilatory nitrate reduction (NO_3^- to NH_4^+) (Butterbach-Bahl et al., 2013; Hu et al., 2015; Kuypers et al., 2018; Wrage-Mönnig et al., 2018; Kumar et al., 2020; Prosser et al., 2020). These processes are carried out by different microorganisms including archaea, bacteria, and fungi while the transformations of N compounds are catalyzed by different enzymes encoded by distinct functional genes (e.g. Hu et al., 2015; Kuypers et al., 2018; Kumar et al., 2020). Among these functional genes, *amo*A (gene encoding ammonium monooxygenase), *nxr*B (gene encoding nitrite oxidoreductase), *nar*G (gene encoding nitrate reductase), *nir*K/*nir*S (gene encoding nitrite reductase), and *nos*Z (gene encoding N_2O reductase) have been most frequently investigated (Butterbach-Bahl et al., 2013; Hu et al., 2015; Norton and Ouyang, 2019; Storch et al., 2023).

Several authors investigated soil microbial communities and their related N_2O production potential in various cropping systems (e.g. Hamonts et al., 2013; López-Lozano et al., 2017; Dong et al., 2018; Hou et al., 2018; Jones et al., 2022; Deveautour et al., 2022; Yang et al., 2022; Storch et al., 2023). However, little is known about the microbial N_2O production influenced by different fertilizer application types and irrigation systems. Therefore, eight treatments in terms of no (zero) irrigation with and without (zero) broadcasted N fertilizer (ZI-N and ZI-ZN), sprinkler irrigation with and without (zero)

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broadcasted N fertilizer (SI-N and SI-ZN), drip irrigation with and without (zero) broadcasted N fertilizer (DI-N and DI-ZN) as well as fertigation (F) and fertigation without (zero) crops (F-ZC) were established in a potato cropping system. The objective of this study was to elucidate the underlying genetically determined microbial-mediated pathways of N_2O formation depending on the type, amount, and time of water and fertilizer application. It was firstly hypothesized, that N_2O flux rates differ between the treatments exhibiting lowest flux rates under ZI-ZN and higher N_2O flux rates under sprinkler and drip irrigation (SI-ZN, DI-ZN) due to a higher soil water content and therefore an enhanced denitrification process. Secondly, regarding the different N fertilization regimes, it was hypothesized that the application of several small N doses in irrigation water by fertigation (F) will lead to lower N_2O flux rates compared to the broadcasted N applications (SI-N, DI-N) due to better N use efficiency of the potato crops.

2 Materials and methods

2.1 Experimental site and N_2O flux measurement

The study was conducted at the Field Research Station of the Leibniz Institute for Agricultural Engineering and Bioeconomy in Marquardt (Federal State Brandenburg, Germany; 52°28'02" N 12°57'37" E). N_2O measurements started three weeks after potatoes were planted, covering an entire cropping season of 16 weeks from May 26th to September 15th, 2020. The average annual temperature in 2020 at the Field Research Station was 11.6°C with a mean annual precipitation of 407 mm. The soil is characterized as loamy sand, with 76% sand, 13% clay, 12% silt, with an organic carbon (C_{org}) content of 0.5% and a pH value of 6.75.

Eight different management variants, each in three replicates (plots), were established in a complete randomized block design. The treatments covered eight combinations of varying temporal and spatial distribution of water and nitrogen supply which reflected current application technologies and consisted of: zero irrigation with and without (zero) N application (ZI-N, ZI-ZN), sprinkler irrigation with and without (zero) N application (SI-N, SI-ZN), drip irrigation with and without (zero) N application (DI-N, DI-ZN), and fertigation (simultaneous application of water and N fertilizer) with and without (zero) crops (F, F-ZC) (Table 1).

For drip irrigation, NETAFIM™ Streamline™ X 16080 tubes were installed on the ridges; for sprinkler irrigation, GARDENA® ZoomMaxx was installed in the centre of the respective plots. The amount of irrigation water has been adapted to the site-specific drip irrigation and fertigation system. Drip irrigated plots received 37 L m^{-2}, fertigated plots 59 L m^{-2}, and sprinkler irrigated plots 120 L m^{-2} of water (supplementary Table S1).

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Table 1: Variants of irrigation and fertilization with corresponding temporal and spatial distribution of water and nitrogen supply. For details see Table S1 (supplement) giving an overview of water and nitrogen (N) fertilizer application with indication of the date and amount during the season.

variant	irrigation	N fertilization	distribution of water supply		distribution of N supply	
			temporal	spatial	temporal	spatial
ZI-ZN	no irrigation	no N fertilization	stochastic (rainfall)	homogeneous	stochastic (mineralization of organic matter)	homogeneous
ZI-N	no irrigation	N fertilization (optimal 150 kg/ha)	stochastic (rainfall)	homogeneous	three times per season (75 kg/ha first-order foliation, 45 kg/ha beginning of tuberization and 30 kg/ha maturation)	homogeneous
SI-ZN	sprinkling irrigation	no N fertilization	irregularly in addition to rainfall	homogeneous	stochastic (mineralization of organic matter)	homogeneous
SI-N	sprinkling irrigation	N fertilization (optimal 150 kg/ha)	irregularly in addition to rainfall	homogeneous	three times per season (75 kg/ha first-order foliation, 45 kg/ha beginning of tuberization and 30 kg/ha maturation)	homogeneous
DI-ZN	drip irrigation	no N fertilization	irregularly in addition to rainfall	punctual in grid knot pattern	stochastic (mineralization of organic matter)	homogeneous
DI-N	drip irrigation	N fertilization (optimal 150 kg/ha)	irregularly in addition to rainfall	punctual in grid knot pattern	three times per season (75 kg/ha first-order foliation, 45 kg/ha beginning of tuberization and 30 kg/ha maturation)	homogeneous
F	fertigation (optimal N fertilization 150 kg/ha)		regularly in short intervals (5 to 15 mm every week) in addition to rainfall	punctual in grid knot pattern	regularly in short intervals (about 5 to 15 kg/ha every week)	punctual in grid knot pattern
F-ZC	fertigation, no crops (optimal N fertilization 150 kg/ha)		regularly in short intervals (5 to 15 mm every week) in addition to rainfall	punctual in grid knot pattern	regularly in short intervals (about 5 to 15 kg/ha every week)	punctual in grid knot pattern

ZI = no (zero) irrigation, SI = sprinkling irrigation, DI = drip irrigation, ZN = no (zero) N fertilization, N = location-typical fertilization, F = fertigation, ZC = no (zero) crops.

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Prior to potato planting, all plots were once fertilized with potassium (250 kg K ha^{-1}), magnesium (60 kg Mg ha^{-1}), and sulphur (170 kg S ha^{-1}) (Roschke et al., 2000) using Patentkali®. Throughout the season, N fertilizer Yara Liva Tropicote (chemical composition: 15 % total N, 14.4 % nitrate N, 1.1 % ammonium N, and 25 % water soluble calcium oxide) was applied three times (total amount of N: 150 kg N ha^{-1}) in all fertilized plots, except for the fertigated plots, where fertilizer (Yara Liva Calcinit, 15.5% total N, 14.4% nitrate N, 1.1% ammonium N, and 26% water soluble calcium oxide) was dissolved in the irrigation water and applied in regular intervals (total amount of N: 151 kg N ha^{-1}) (supplementary Table S1). Agrochemicals in terms of fungicides (Acrobat® Plus WG, 2 kg ha^{-1}), insecticides (Biscaya®, 0.3 L ha^{-1}), and herbicides (Boxer®, 5 L ha^{-1}) were applied according to common practice while all plots were treated equally including F-ZC. Additionally, all plots were weeded manually on a weekly basis or when necessary. Except for few weeds, plots of the treatment F-ZC showed bare soil.

The soil-borne N_2O fluxes were measured weekly using the closed chamber method (Trost et al., 2014; Storch et al., 2023). N_2O flux rates were calculated according to Flessa et al. (1998). During gas sampling, soil temperature was measured every 20 min with a penetration thermometer (Testo SE & Co. KGaA, Titisee-Neustadt, Germany) for the ridge (0–10 cm). For statistical analysis, the mean soil temperature per sampling day was calculated.

2.2 Analysis of mineral nitrogen and soil moisture

For each treatment, five soil samples (0–20cm soil depth) per plot were taken weekly to analyse the mineral N (N_{min}) content, including ammonium (NH_4^+), nitrate (NO_3^-), and nitrite (NO_2^-) according to VDLUFA (1991). The determination of volumetric water content (VWC) and bulk density was carried out as described in Storch et al. (2023). From these values, the water filled pore space (WFPS) was determined according to Linn and Doran (1984).

2.3 Analysis of mineral nitrogen and soil moisture

For profiling the functional genes within the N cycle, five distinct sample dates out of the entire vegetation period were analysed. These dates corresponded to the seasonal development of N_2O fluxes while simultaneously covering the different crop developmental stages including the early vegetative period with strong growth rate, the transition from vegetative to flowering period, and the maturation and senescence period. Per plot, three soil cores at a depth of 0–10 cm (ridge) were taken in the rhizosphere of the potato crops with a geological drill.

Total genomic DNA was extracted using the FastDNA™ Spin Kit for Soil (MP Biomedicals GmbH, Germany) as specified by the manufacturer. For each soil sample per plot, three DNA extractions were carried out. The different microbial-mediated pathways within the N cycle, especially those related to N_2O emissions, were analyzed by using pathway-specific quantitative real-time polymerase chain reaction (qPCR) approaches to quantify the gene copy numbers per gram soil of *amo*A (encoding ammonium monooxygenase), *nxr*B (encoding nitrite oxidoreductase), *nar*G (encoding nitrate reductase), *nir*S/*nir*K (encoding nitrite reductase), and *nos*Z (encoding N_2O reductase). The following specific primer sets were used: amoA3F/amoA-5R for *amo*A, (amplicon size: 238 bp), nxrB169f/nxrB638r for *nrx*B (amplicon size: 484 bp),

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narG572f/narG773r for *nar*G (amplicon size: 201bp), F1aCU/R3CU for *nir*K (amplicon size: 472 bp), Cd3aF/R3cd for *nir*S (amplicon size: 416 bp), and nosZ2F/mosZ2R for *nos*Z amplicon size: 700 bp) (for details see Supporting Information Table S3 in Storch et al., 2023).

2.4 Statistical analysis

The individual seasonal development of N_2O fluxes per treatment was analyzed by an ANOVA, based on a generalized linear mixed effect model using the package `glmmTMB´ (Brook et al., 2017) of the R statistical software (R Core Team, 2020) including RStudio program (RStudio Team, 2021). For time-dependent determination of microbial impacts on N_2O emissions within the different treatments, detected gene copy numbers were analyzed by applying a generalized linear model using the packages `nlme´ (Pinheiro and Bates, 2000), followed by a two-way ANOVA with Tukey post-hoc test. The distinct sample dates for microbial analysis were unevenly spaced in time. Therefore, an exponential correlation (corEXP) function was fitted to model temporal correlations between N_2O emissions and microbial data. For time-independent analysis, Pearson's correlations were performed by using `rstatix´ package (Kassambara, 2021) in R statistical software (R Core Team, 2020) to explore the relationships between environmental factors, microbial gene copy numbers, and $N_2O$ emissions. Additionally, a nonmetric multidimensional scaling (NMDS) using the package `vegan´ (Oksanen et al., 2017), was used to identify main influencing factors on functional genes. Therefore, data was transformed using square root transformations and standardized using Wisconsin double standardization.

3 Results and discussion

3.1 N_2O flux rates influenced by different irrigation and fertilization regimes

As expected, the control (ZI-ZN, no irrigation, no fertilization) showed the lowest N_2O fluxes throughout the season. The seasonal median N_2O fluxes across all treatments ranged from 8.16 µg N_2O-N m^{-2} h^{-1} (ZI-ZN) to 23.58 µg N_2O-N m^{-2} h^{-1} (F) (Fig. 1, supplementary Table S2). These values are in a narrower range compared to values found on the same study site in 2019 (Storch et al., 2023).

The median cumulative N_2O emissions ranged from 0.38 to 0.83 kg N_2O-N m^{-2} h^{-1}. Only the treatment without potato crops showed lower cumulative N_2O emissions (0.3 kg N_2O-N m^{-2} h^{-1}). These values are partly exceeding the common range of N_2O fluxes and cumulative N_2O emissions found in earlier studies on sandy soils and potato cropping (Trost et al., 2014; Mathivanan et al., 2021; Thilakarathna et al., 2022). This might be explained by the used gas sample chambers, as these chambers included the ridge as well as the furrow. The study by Thilakarathna et al. (2022) shows that generally a higher amount of N_2O is produced in the furrow compared to the ridges. This effect might be enhanced when irrigation water is applied.

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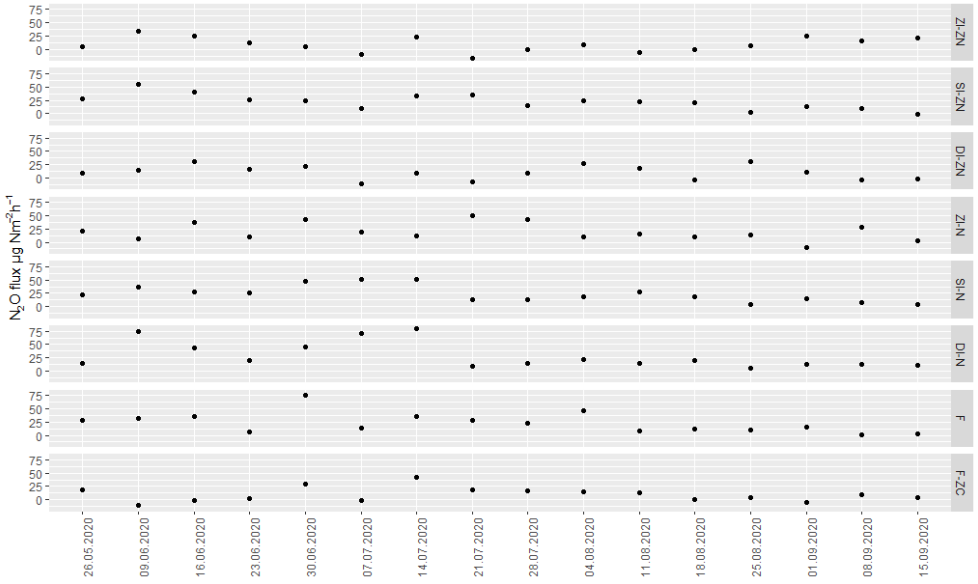

Figure 1: Median N_2O fluxes (dots) during the potato cropping season in 2020 for the different treatments: Abbreviations: ZI-ZN = zero irrigation without (zero) nitrogen (N) fertilizer, ZI-N = zero irrigation with broadcasted nitrogen (N) fertilizer, SI-ZN = sprinkler irrigation without (zero) nitrogen (N) fertilizer, SI-N = sprinkler irrigation with broadcasted nitrogen (N) fertilizer, DI-ZN = drip irrigation without (zero) nitrogen (N) fertilizer, DI-N = drip irrigation with broadcasted nitrogen (N) fertilizer, F = fertigation, F-ZC = fertigation without (zero) crops.

A global meta-analysis conducted by Kuang et al. (2021) indicated that N_2O emissions under sprinkler irrigation are 46% higher compared to drip irrigation. In the present study, this effect and hence the first hypothesis can be confirmed. Lowest N_2O emissions originated from the non-irrigated and drip irrigated plots and were within the same range of median cumulative N_2O emissions (ZI-ZN: 0.4 kg N_2O-N ha^{-1}; DI-ZN: 0.38 kg N_2O-N ha^{-1}), while the median cumulative N_2O emission on sprinkler irrigated plots were approximately 65% higher (SI-ZN: 0.63 kg N_2O-N ha^{-1}). This is further confirmed by the fact that the sprinkler irrigated plots (SI-ZN) showed a 2.4-fold and 3.2-fold higher N2O flux rate (based on the seasonal median N^2O flux rate values) compared to the drip irrigated plots (DI-ZN) and the untreated reference plots (ZI-ZN) (Fig. 1, supplementary Table S2). The fertilizer application in ZI-N, SI-N, DI-N, and F led to an increase of N_2O flux rates by a factor of two to three compared to the untreated reference treatment (ZI-ZN), while the application type of water and fertilizer (broadcasted application under sprinkler or drip irrigation or dissolved in irrigation water within fertigation) had only minor effects on N_2O flux rates (supplementary Table S2).

Under sprinkler irrigated treatments (SI-ZN and SI-N) the highest water volumes were applied (supplementary Table S1) leading to the highest N_2O flux rates (Fig. 1, supplementary Table S2). Even though these agronomic measures generally meet the crop demand of water and N according to good agricultural practice (DüProNP, 2023), maybe the time of application could be adapted, considering that the potatoes mainly require N at later growth stages (Ierna and Mauromicale, 2018; Milroy et al., 2019; Kuang et al., 2021; Grandy et al., 2022), which simultaneously could also mitigate N_2O emissions.

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Compared to the sprinkler irrigated plots, N_2O fluxes were lower in drip irrigated plots (DI-ZN, DI-N and F), while the application of dissolved N fertilizer directly into the root zone in multiple small applications during crop growth (F) had no further positive effects on N_2O emission reduction (Fig. 1, supplementary Table S2). This latter observation might be attributed to the different nutrient uptake capacities during the potato growth stages with appr. 15% during the vegetative stage, 30% during tuber initiation stage, and 58-71% during tuber bulking stage (Ojala et al., 1990; Ierna and Mauromicale, 2018). This indicates that even under fertigation the supply of N fertilizer should be better adapted to the crop demands. However, in all investigated treatments, except for the untreated reference plots ZI-ZN and the fertigated plots without crops (F-ZC), generally higher N_2O flux rates were detected during the first half of the cropping season (supplementary Table S3). This might be inter alia explained by a higher N availability for microorganisms during the vegetative stage, when potato crops have a lower nutrient uptake capacity (Ojala et al., 1990; Ierna and Mauromicale, 2018). Within the second half of the growing season N_2O flux rates decreased presumably due to a higher N uptake capacity of potato plants, which were in tuber initiation and tuber bulking stage. This assumption is in accordance with results from maize and wheat, where more than 60% of total seasonal N_2O fluxes occurred during the vegetative stage (Dhadli et al., 2016). However, the lowest N_2O flux rates were detected for the treatment F-ZC (fertigation without (zero) crops) although the supplied N was exclusively available for the microbial community. This indicates an impact of the cultivated crops and their interaction with the N_2O producing microorganisms. There is evidence that crops affect the assemblage of the microbiome in the soil and rhizosphere by serving as a carbon source for microorganisms (e.g. el Zahar Haichar et al., 2016; Sasse et al., 2018). Moreover, root exudates also affect N transformation processes, with inter alia inhibiting effects on nitrification and denitrification processes (Hou et al., 2018; Moreau et al., 2019; Fan et al., 2022; Grandy et al., 2022).

3.2 Effects on functional genes within the bacterial N cycle in applied management regimes– NMDS

A nonmetric multidimensional scaling (NMDS) was carried out to identify (dis-)similarities between the different management systems over the entire growing season based on the quantities of the six investigated functional genes per sampling point (Fig. 2). This analysis revealed a time-dependent clustering, separating the first and the second half of the season independent of the treatment. Regarding the first half of the season, the quantities of detected *amo*A and *nar*G gene copy numbers per gram soil were mostly responsible for the ordination configuration of the samples. Additionally, N_2O as the environmental variable of most interest showed strong correlations within this ordination configuration. Therefore, N_2O as dependent variable could be explained by the respective ordination scores (Fig. 2). This observation is supported by several studies showing that fertilizer application favours ammonia-oxidizing bacteria and correspondingly might enhance the potential of nitrification-derived N_2O production (Bertagnolli et al., 2016; Hink et al., 2018; Wang et al., 2016; Liang and Robertson, 2021). Hence, the measured N_2O fluxes during the first half of the season were most probably a product of a coupled nitrification-denitrification process. This proves the previous assumption that higher flux rates within the first half of the season might be attributed to the relation between higher N availability for microorganisms and lower nutrient uptake by plants (Ojala et al., 1990; Ierna and Mauromicale, 2018).

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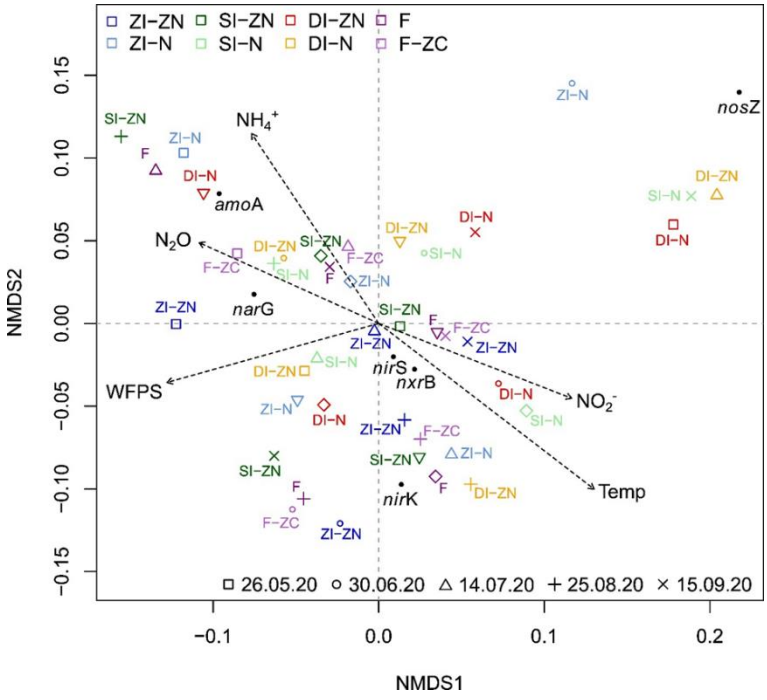

Figure 2: Non-metric multidimensional scaling (NMDS) analysis based the detected copy numbers per gram soil of the investigated genes *amo*A (encoding ammonium monooxygenase), *nxr*B (encoding nitrite oxidoreductase), *nar*G (encoding nitrate reductase), *nir*K/*nir*S (encoding nitrite reductase) and *nos*Z (encoding nitrous oxide reductase). Each colour symbolizes one of the investigated treatments: dark blue = ZI-ZN (no (zero) irrigation without (zero) nitrogen (N) fertilizer), light blue = ZI-N (no (zero) irrigation with broadcasted nitrogen (N) fertilizer), dark green = SI-ZN (sprinkler irrigation without (zero) nitrogen (N) fertilizer), light green = SI-N (sprinkler irrigation with broadcasted nitrogen (N) fertilizer), red = DI-ZN (drip irrigation without (zero) nitrogen (N) fertilizer), orange = DI-N (drip irrigation with broadcasted nitrogen (N) fertilizer), dark purple = F (fertigation), light purple = F-ZC (fertigation without (zero) crops). Symbols are used to indicate the different time points. Marked with a black dot (●) are symbolizing investigated functional genes. The given environmental vectors (arrows) symbolize the measured environmental parameters in terms of soil temperature (Temp), water filled pore space (WFPS), soil ammonium content (NH_4^+), soil nitrite content (NO_2^-) and the N_2O flux rates (N_2O).

3.3 Effects of different irrigation technologies on the bacterial N cycle

The different microbial mediated N_2O production pathways depend on the occurrence of microorganisms harbouring the respective process-related genes encoding the acting enzymes. The microbial community composition in general is influenced by several environmental factors fluctuating seasonally and temporally, causing highly variable N_2O emissions (e.g. Butterbach-Bahl et al., 2013; Hu et al., 2015; Kuypers et al., 2018; Storch et al., 2023). One of the most important driving factors for the N_2O release from soils is the availability of oxygen (O_2), which negatively correlates with the soil water content (Schaufler et al., 2010; Butterbach-Bahl et al., 2013; Hu et al., 2015). In this regard, irrigation in general leads to an increase in the soil water content and hence anaerobic conditions, which might stimulate the microbial N_2O production via the denitrification pathway (Butterbach-Bahl et al., 2013; Trost et al., 2013; Hu et al., 2015; Kuang et al., 2021). For the

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genetically determined denitrification process the three enzymes nitrate reductase, nitrite reductases, and nitrous oxide reductase with their corresponding genes *nar*G, *nir*K/*nir*S and *nos*Z are frequently considered in relation to N_2O production (Hu et al., 2015; Kuypers et al., 2018).

Regarding the seasonal development of the functional gene quantities in the untreated reference plots (ZI-ZN), a significant decrease of the *nar*G gene copy number g^{-1} soil over the cropping season was detected, while no significant seasonal changes were found for either the *nir*K or *nir*S gene copy number g^{-1} soil. The *nos*Z gene copy number g^{-1} soil significantly decreased during the second half of the season (supplementary Fig. A1 and Table S4). Additionally, Pearson analysis revealed a moderate negative correlation between the *nir*S and *nos*Z gene copy numbers g^{-1} soil (r = -0.550), but a strong positive correlation between the *nir*S gene copy number g^{-1} soil and the detected N_2O flux rates (r = 0.641) (Fig. 3, supplementary Table S5). Therefore, the microbial community in the untreated reference ZI-ZN seemed to be dominated by *nir*S-type microorganisms which potentially were responsible for the detected N_2O fluxes. However, as most of the detected correlations between the investigated genes were negative, a clear pathway of the N_2O formation cannot be derived (Fig. 3 supplementary Table S5).

Highest N_2O flux rates were detected under sprinkler irrigation (SI-ZN), suggesting that the increased soil water content stimulated the N_2O production, particularly during the first half of the season (Fig. 1). Contrary to the hypothesis that higher water volumes result in a stimulation of the process of denitrification, the detected correlation patterns of the investigated genes showed that denitrification was unlikely the underlying pathway of N_2O production under SI-ZN (Fig. 3, supplementary Table S6). It is more probable that environments with fluctuating aerobic-anaerobic conditions under sprinkler irrigation systems promote N_2O production by nitrifier denitrification (Wrage-Mönnig et al., 2018). During the first step, NH_4^+ is oxidized to hydroxylamine (NH_2OH) which is further oxidized to nitric oxide (NO) (Hu et al., 2015; Caranto and Lancaster, 2017; Kuypers et al., 2018; Prosser et al., 2020) and subsequently to N_2O (Wrage-Mönnig et al., 2018; Prosser et al., 2020). In this regard, the *amo*A gene copy number g^{-1} soil showed a significant increase during the first half of the cropping season (supplementary Fig. S1 and Table S4), while the Pearson analysis revealed a positive correlation with the detected N_2O flux rates (r = 0.321) (Fig. 3, supplementary Table S6). In addition, *amo*A gene copy number g^{-1} soil negatively correlated with the *nxr*B gene copy number g^{-1} soil (r = 0.576), but positively correlated with the *nar*G gene copy number g^{-1} soil (r = 0.591) (Fig. 3, supplementary Table S6). It has to be noted that the *nxr* and *nar* genes show structural similarities and hence their corresponding enzymes have most likely comparable metabolic capacities as they not only convert NO_2^- to NO_3^- but they might also enable the oxidation of NO_3^- to NO_2^- (Maia and Moura, 2014; Kuypers et al., 2018). However, the *nxr*B gene copy number g^{-1} soil positively correlated with *nir*K and the *nir*S gene copy numbers g^{-1} soil (r = 0.880, r = 0.560), while the *nir*S gene copy numbers g^{-1} soil in turn positively correlated with the *nos*Z gene copy number g^{-1} soil (r = 0.519) (Fig. 3, supplementary Table S6). Moreover, the *nir*K and the *nir*S gene copy numbers g^{-1} soil further correlated moderately to strongly negative to the detected N_2O flux rates (r = -0.566, r = -0.896) (Fig. 3, supplementary Table S6). Therefore, it can be assumed that the N_2O release of SI-ZN was not relatable to the process of denitrification, but more likely to the nitrifier denitrification.

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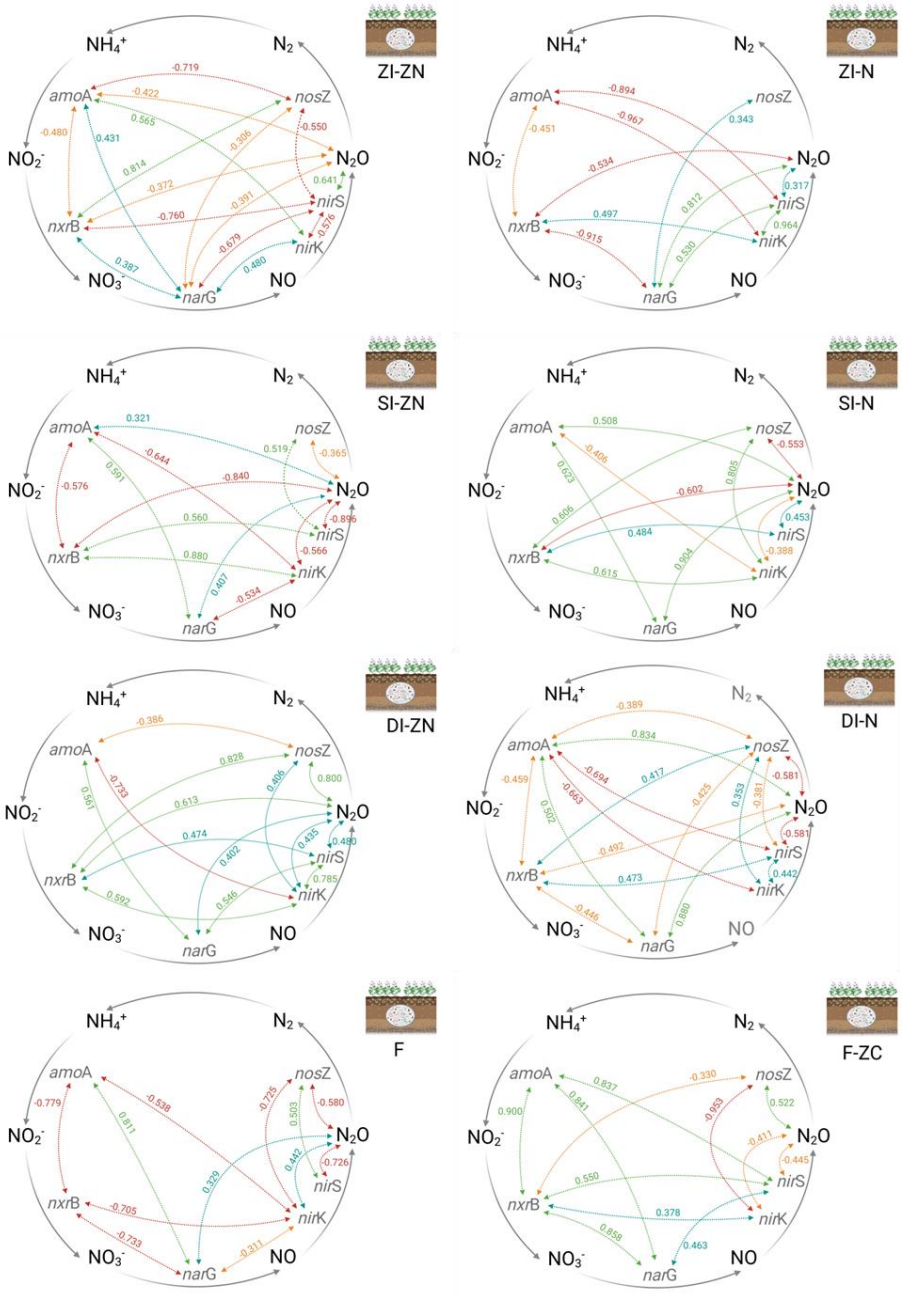

Figure 3: Pearson's correlations for the detection of time-independent relationships between the recorded gene copy numbers per gram soil and N_2O flux rates of the ridge (0-10cm). Shown are weak (≥ 0.30), moderate (≥ 0.50) and strong (≥ 0.75) positive (green) and negative (red) correlations. Abbreviations: ZI-ZN = zero irrigation without (zero) nitrogen (N) fertilizer, ZI-N = zero irrigation with broadcasted nitrogen (N) fertilizer, SI-ZN = sprinkler irrigation without (zero) nitrogen (N) fertilizer, SI-N = sprinkler irrigation with broadcasted nitrogen (N) fertilizer, DI-ZN = drip irrigation without (zero) nitrogen (N) fertilizer, DI-N = drip irrigation with broadcasted nitrogen (N) fertilizer, F = fertigation, F-ZC = fertigation without (zero) crops, *amo*A = gene encoding ammonium monooxygenase, *nxr*B = gene encoding nitrite oxidoreductase, *nar*G = gene encoding nitrate reductase, *nir*K/*nir*S = genes encoding nitrite reductase and *nos*Z = gene encoding nitrous oxide reductase.

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In contrast to SI-ZN and in accordance with the first hypothesis, the process of denitrification under drip irrigation (DI-ZN) seems to be feasible as the Pearson analysis revealed positive correlations either between the *nxr*B and the *nir*K gene copy numbers g^{-1} soil (r = 0.592), or the *nar*G and the *nir*S gene copy numbers g^{-1} soil (r = 0.546). The gene copy numbers g^{-1} soil of *nxr*B and *nir*K were at the same level throughout the entire season and could further be correlated with the N_2O flux rates (r = 0.613, r = 0.435) (Fig. 3, supplementary Table S7). This indicates that the occurring microbial community was most probably dominated by *nir*K-type microorganisms which often lack the *nos*Z gene and hence produce N_2O as their denitrification end-product (Graf et al., 2014; Lycus et al., 2017). In that case, it can be assumed that higher soil moisture near the drippers lead to anaerobic conditions favouring the process of denitrification whereas the higher frequency of wet-dry-cycles around the drippers further enhanced N_2O production. Therefore, it can be concluded, that water application does stimulate N_2O production compared to the control treatment (ZI-ZN). However, an increase in N_2O flux rates due to water application cannot exclusively be related to the process of denitrification, but also to the process of nitrifier denitrification, which stands partly in contrast with the first hypothesis.

3.4 Effects of different N fertilizer application technologies on the bacterial N cycle

N fertilizer addition (ZI-N, SI-N, DI-N and F) increased N_2O flux rates by a factor of two to three compared to the untreated reference ZI-ZN, whereas the application type of water and fertilizer (SI-N, DI-N and F) had only minor effects on the N_2O flux rates (Fig. 1, supplementary Table S2 and S3).

A clear effect of the N fertilizer addition irrespectively of additional water supply was found in non-irrigated and broadcasted fertilized treatments (ZI-N), where N_2O flux rates were two-fold higher compared to the untreated reference ZI-ZN (supplementary Table S2 and S3). While no clear potential pathway of N_2O formation could be derived for the untreated reference ZI-ZN, the broadcasted N application under ZI-N seemed to stimulate the N_2O production based on the denitrification process. A positive correlation was either found between the *nxr*B and *nir*K gene copy numbers g^{-1} soil (r = 0.497) or between the *nar*G and *nir*S gene copy numbers g^{-1} soil (r = 0.530) (Fig. 3, supplementary Table S8). Additionally, the Pearson analysis revealed a strong positive correlation between the denitrification genes *nir*K and *nir*S (r = 0.964), while the *nir*S itself further positively correlated to the detected N_2O flux rate (r = 0.317) (Fig. 3, supplementary Table S8). Further ANOVA analysis revealed a significant relationship between both the *nar*G and the *nir*S genes gene copy numbers g^{-1} soil and the N_2O flux rates (p = 0.008, p = 0.085) for ZI-N (supplementary Table S13). Additionally, the detected quantities of both genes showed a significant increase during the first half of the season followed by a significant decrease. This is in accordance with results of a meta-analysis conducted by You et al. (2022), who recorded a stimulating effect of N amendment inter alia on the quantities of bacterial denitrification genes.

Moreover, a water supply either by sprinkler irrigation (SI-N) or drip irrigation (DI-N, F) only led to a minor further increase in the N2O flux rates (Fig. 1, appendix Table A2 and A3). Regarding the effects of broadcasted N applications under different irrigation systems (SI-N, DI-N) on the genetically determined functional gene composition, differences in the correlation

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pattern of the investigated genes and hence the possible microbial N_2O production pathways were found (Fig. 3). Surprisingly, the broadcasted N fertilizer application under sprinkler irrigation (SI-N) led to a slight reduction in the N_2O flux rates (Fig. 1, appendix Table A2 and A3). Based on the positive correlation between the *amo*A and *nar*G gene copy numbers g^{-1} soil (r = 0.623) and moreover their individual correlation to the detected N_2O flux rates (r = 0.508, r = 0.904), a nitrifier denitrification can be assumed (Fig. 3, supplementary Table S9). Additionally, positive correlations were found between the *nxr*B gene copy number g^{-1} soil with both denitrification genes *nir*K and *nir*S (r = 0.615, r = 0.484) with a subsequent positive correlation between the *nir*S gene copy number g^{-1} soil and the N_2O flux rates (r = 0.453) (Fig. 3, supplementary Table S9). Therefore, greater N_2O flux rates might have been expected under SI-N compared to SI-ZN. However, the strong positive correlation between the *nir*K and the *nos*Z gene copy numbers g^{-1} soil (r = 0.805) (Fig. 3, supplementary Table S9) indicates a transformation of N_2O to N_2 resulting in lower N_2O flux rates under SI-N. This is in accordance with the study by You et al. (2022), who detected inter alia an increase of *nir*K and *nos*Z under N amendment. In contrast to the sprinkler irrigated treatments (SI-ZN and SI-N), the broadcasted as well as the dissolved N fertilizer supply under drip irrigation (DI-N and F) resulted in an increased N_2O formation (Fig. 1, appendix Table A2 and A3), which stands in contrast to the second hypothesis and the results provided by Kuang et al. (2021). However, a greater frequency of wetting and drying cycles next to the dripper could enhance N_2O production. Therefore, higher N_2O flux rates under drip irrigation in this study could be explained.

N_2O release under drip irrigated unfertilized treatment (DI-ZN) was most probably attributed to a *nxr*B/*nir*K-type dominated bacterial community, whereas under DI-N and F, no clear N_2O production pathway based on the investigated gene quantities and their correlation patterns could be found. Both treatments showed a positive correlation between the *amo*A and *nar*G gene copy numbers g^{-1} soil (r = 0.502 for DI-N, r = 0.811 for F) with subsequent correlation of the *nar*G gene copy number g^{-1} soil and the detected N_2O flux rates (r = 0.880 for DI-N, r = 0.329 for F) (Fig. 3, appendix Table A10 and A11). This indicates that N_2O production might be related to the process of nitrifier denitrification, which is in accordance with the enhancing effects on nitrifier denitrification due to changes between aerobic and anaerobic soil conditions (Wrage-Mönning et al., 2018) as they occur next to the drippers.

The lowest N_2O flux rates were measured for the treatment F-ZC (fertigation without (zero) crops) which is most probably related to the absence of potato crops and hence the non-availability of carbon sources (root exudates) for the soil microorganisms (e.g. el Zahar Haichar et al., 2016; Hou et al., 2018; Sasse et al., 2018; Moreau et al., 2019; Fan et al., 2022; Grandy et al., 2022). However, the correlation patterns of the investigated genes indicated that both the process of nitrification and denitrification could have been carried out (Fig. 3). For example, the Pearson analysis revealed positive relationships of the *amo*A gene copy number g^{-1} soil with the *nxr*B and *nar*G gene copy numbers g^{-1} soil (r = 0.900, r = 0.841) indicative for the nitrification pathway, whereas the positive correlations between the *nxr*B and both *nir*K and *nir*S gene copy numbers g^{-1} soil (r = 0.378, r = 0.550) as well as between the *nar*G and *nir*S gene copy numbers g^{-1} soil (r = 0.463) indicated the potential for the denitrification pathway (Fig. 3, appendix Table A12). However, the negative correlations of the *nir*K and *nir*S gene copy

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numbers g^{-1} soil and the N_2O flux rates might explain the low N_2O flux rates in general (r = -0.411, r = -0.445) (Fig. 3, appendix Table A12).

3.5 Summarized assessment of the genetically determined N2O production pathways within the applied management regimes

This study elucidated the potentially occurring bacterial-mediated pathways of N_2O release from sandy agricultural soils affected by different irrigation and nitrogen fertilization regimes in potato cropping. The N_2O flux rates in this study were mostly affected by the amount of additionally supplied water with highest N_2O flux rates under sprinkler irrigation (received 120 L m^{-2}) compared to drip irrigation (received 37 L m^{-2}) and fertigation (received 57 L m^{-2}) instead of the type and mode of N fertilizer application (broadcasted application vs. dissolved in irrigation water, all received 150 kg N ha^{-1}). These differences in the detected N_2O flux rates are generally in accordance with the first hypothesis that an additional water supply led to higher N_2O fluxes. However, it has been shown that higher water volume application does not exclusively result in stimulating the denitrification processes but rather the process of nitrifier denitrification. A comparison of the impact of solely sprinkler irrigation (SI-ZN) and solely N fertilizer (ZI-N) on the potential pathways of N_2O formation revealed two different options in terms of nitrifier denitrification for SI-ZN or a *nir*S-type denitrification for ZI-N, whereas the combined application of sprinkler irrigation and N fertilizer (SI-N) potentially promoted N_2O production related to both pathways. Moreover, the comparison of the different water application types (sprinkler vs. drip irrigation; SI-ZN vs. DI-ZN) indicated a predominating *nxr*B-*nir*K-type denitrification under drip irrigation, which can be most probably related to stronger pronounced anaerobic conditions due to higher soil moisture near the drippers. Therefore, the first hypothesis can only partly be proven in this study. The type of N fertilizer supply, broadcasted application or dissolved in irrigation water (DI-N vs. F), showed only minor differences in the potential microbial community functionality. N_2O production in both treatments was most probably dominated by nitrifier denitrification, while for DI-N a *nxr*B-*nir*K/*nir*S-type denitrification might also be feasible. This stands in contrast to the hypothesized better N use efficiency under fertigated systems resulting in lower N_2O emissions. However, generally higher N_2O flux rates were detected during the first half of the cropping season due to higher N availability for microorganisms during the vegetative stage of the potatoes, while the N_2O flux rates decreased during the second half of the season when the potato crops have higher N uptake. In this regard, a similarity analysis revealed that the bacterial-mediated N_2O release was dominated by nitrifier denitrification during the first half of the season due to the fact that fertilizer application favours ammonia-oxidizing bacteria and correspondingly enhance the potential of nitrification-derived N_2O production.

4 Conclusion

The different irrigation and fertilization technologies applied in this study led to different N_2O flux rates over the entire cropping season with highest flux rates during the first half of the season. Regarding the underlying genetically determined

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N_2O production pathway, this study indicates that the nitrifier denitrification process is of great importance. Further research is required to adjust the amount and time of water and N fertilizer application based on crop demand for nutrients and their related use efficiency during the different crop growth stages. It might be recommended to adapt the time of N application, considering that potatoes mainly require N at later growth stages, which simultaneously could also reduce N_2O emissions.

Authors contribution (according to CRediT): Conceptualization: LCS, ST, AP, BT, LR; Investigation (agronomy): KS; Investigation (functional profiling): LCS; Formal Analysis (agronomy): KS; Formal Analysis (functional profiling): LCS; Formal Analysis (system ecological analyses): LCS, ST; Visualization: LCS, ST, Writing – original draft: LCS, ST, Writing – review & editing: KS, JK, AP, LR, BT; Funding acquisition: BT, LR, ST, AP, Project administration: BT, LR, ST, Supervision: ST. All authors have read and agreed to the published version of the manuscript.

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