Evaluating N₂O Emissions and Carbon Sequestration in Temperate Croplands with Cover Crops: Insights from Field Trials

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Abstract. Cover Crops (CCs) are acclaimed for enhancing the environmental sustainability of agricultural practices by aiding in carbon (C) sequestration and reducing losses of soil mineral nitrogen (SMN) after harvest. Yet, their influence on nitrous oxide (N₂O) emissions - a potent greenhouse gas - presents a complex challenge, with findings varying across different studies. This research aimed to elucidate the effects of various winter CCs - winter rye (frost tolerant grass), saia oat (frost sensitive grass), and spring vetch (frost sensitive legume) - compared to a bare fallow control on SMN dynamics, N₂O emissions and C sequestration. These effects were determined by measuring SMN dynamics and N₂O emissions in field experiments. The effects of CCs on soil C sequestration over a 50-year period were predicted by soil organic C (SOC) models using measured above- and below-ground CC biomass. While CCs efficiently lowered SMN levels during their growth, they slightly increased N₂O emissions compared to bare fallow. In particular, winter frost events triggered significant emissions from the frost-sensitive varieties. Moreover, residue incorporation and tillage practices were associated with increased N₂O emissions in all CC treatments. Winter rye, characterized by its high biomass production and nitrogen (N) uptake, was associated with the highest cumulative N₂O emissions, highlighting the influence of biomass management and tillage practices on N cycling and N₂O emissions. The CC treatment resulted in a slight increase in direct N₂O emissions (4.5±3.0, 2.7±1.4, and 3.1±3.8 kg N₂O-N ha^{-1} for rye, oat, and vetch, respectively) compared to the fallow (2.6±1.7 kg N₂O-N ha^{-1}) over the entire trial period (18 months). However, the potential of non-legume CCs to reduce indirect N₂O emissions compared to fallow (0.3±0.4 and 0.2±0.1 kg N₂O-N ha^{-1} a^{-1} for rye and oat respectively) and their contribution to C sequestration (120-150 kg C ha^{-1} a^{-1} over a period of 50 years when CCs were grown every fourth year) might partially counterbalance these emissions. Thus, while CCs provide environmental benefits, their net impact on N₂O emissions requires further research into optimized CC selection and management strategies tailored to specific site conditions to fully exploit their environmental advantages.

1 Introduction

The use of cover crops (CCs) is currently being strongly promoted in many countries due to the multifaceted agro-ecological
35 benefits they offer. They positively influence soil physical, chemical, and biological properties, enhancing soil water retention and aiding in weed and disease control through competitive interactions and pest cycle disruptions (Adetunji et al., 2020; Araújo et al., 2021). The incorporation of CC residues boosts soil microbial biomass and activity, thereby enriching biodiversity and providing habitats for beneficial insects (Elhakeem et al., 2019; Finney et al., 2017). When managed effectively, CCs can enhance the yield of subsequent main crops (Adetunji et al., 2020). Grunwald et al. (2022) observed that
40 cover-cropping prior to sugar beet cultivation improved soil physical properties, facilitating early growth of sugar beet, which is crucial for high sugar yields (Malnou et al., 2006). However, the effect of CCs on soil water storage, succeeding crop yield, and water-use efficiency may not be consistent in all regions (Wang et al., 2021).

Cover crops may also influence nitrous oxide (N_2O) emissions, a potent greenhouse gas. The agricultural sector accounts for about 60% of global anthropogenic N_2O emissions (Masson-Delmotte et al., 2021). These emissions have increased since 1980
45 due to increased nitrogen (N) fertilizer and manure usage (Davidson, 2009; Tian et al., 2020). Approximately half of the N applied to agricultural fields is absorbed by crops, while the remainder is subject to loss into the atmosphere as NH_3, NO, N_2O and N_2 or loss to groundwater and surface water primarily in the form of nitrate (NO_3^-) (Galloway and Cowling, 2002). In temperate regions, N losses are exacerbated during periods of high precipitation (Gabriel and Quemada, 2011). Cover crops can mitigate these losses by absorbing excess soil mineral N (SMN) after harvest (Abdalla et al., 2019), reducing NO_3^- leaching
50 and runoff, and thereby reducing the need for N fertilization in subsequent crops (Constantin et al., 2011; Hanrahan et al., 2021; Nouri et al., 2022; Tonitto et al., 2006). Leguminous CCs further contribute to soil N through atmospheric fixation (Parr et al., 2011). They may also aid in carbon (C) sequestration when used as green manure, enhancing soil C stocks (Poeplau and Don, 2015). Nevertheless, studies on the net effects of CCs on N_2O emissions have yielded mixed results (Basche et al., 2014; Guenet et al., 2021).

55 Cover crop residue management and soil cultivation practices play a crucial role in N_2O emission dynamics and magnitudes. Frost-tolerant CCs can be terminated using various methods in preparation for the next cash crop, while frost-sensitive ones are typically terminated by winter frosts (Storr et al., 2021; Wayman et al., 2015). In some cases, greater soil disturbance in conventional tillage was found to increase N_2O emissions compared to reduced tillage or no-till (Chatskikh et al., 2008). On the other hand, ploughing of heavy soils was found to significantly reduce N_2O emissions (Rochette et al., 2008). Soil
60 incorporation of CC residues increases N_2O emissions compared to surface placement, likely due to accelerated decomposition following increased contact with soil microorganisms (Basche et al., 2014; Lynch et al., 2016).

Crop residues are generally seen as contributors to N_2O emissions because of their N and C content. According to the IPCC (2019), about 1% of the N in crop residues is converted to N_2O. The biochemical properties of CCs, such as the C:N ratio, are critical in influencing residue decomposition rates and subsequent N_2O emissions (Lynch et al., 2016). Residues with lower
65 C:N ratio are decomposed faster, leading to higher N_2O emissions (Basche et al., 2014; Chen et al., 2013; Fosu et al., 2007).

The developmental stage of CCs at termination is also relevant due to its impact on residue composition and the amount of N_2O emissions after incorporation (Balkcom et al., 2015). Early termination of CCs, which are typically characterized by lower C:N ratios, results in higher N_2O emissions (Abalos et al., 2022). Legume CCs generally have lower C:N ratios and result in higher N_2O emissions than non-legumes (Basche et al., 2014; Muhammad et al., 2019).

70   While crop residue quality plays the biggest role in predicting crop residue-induced N_2O emissions, environmental factors such as soil pH, soil N, available soil organic C (SOC), water-filled pore space (WFPS) and temperature also play a role (Abalos et al., 2022). In addition, in temperate cold humid zones, freeze-thaw cycles can lead to significant N_2O emission peaks, contributing substantially to the annual cropland N_2O emissions in these regions (Goodroad and Keeney, 1984; Lemke et al., 1998; Wagner-Riddle et al., 2017).

75   In numerous meta-studies it has been shown that CCs increase SOC stocks (Abdalla et al., 2019; Blanco-Canqui, 2022; Blanco-Canqui et al., 2015; Bolinder et al., 2020; Poeplau and Don, 2015). Thus, soil C sequestration from CCs needs to be considered when assessing the effect of CCs on GHG emissions from croplands. The magnitude of GHG savings depend on site-specific conditions and additional C inputs from CCs. Carbon turnover models have been applied to model effects of CCs on SOC sequestration (Poeplau and Don, 2015; Seitz et al., 2023). In these model applications, the modelled effects are sensitive to the

80   additional C inputs from CCs that vary between CC species.

The objectives of this study were to assess how CC species—differing in frost tolerance and biochemical composition—influence both short-term and long-term N_2O emissions and SMN dynamics in a CC–sugar beet–winter wheat rotation on Luvisol soils, a common substrate for sugar beet cultivation in Germany. We also aimed to identify key drivers of N_2O emissions, including soil temperature, moisture, SMN concentrations, and the quantity and composition of incorporated CC

85   biomass, to weigh the benefits and drawbacks of cover cropping with respect to N_2O emissions, SMN dynamics, and SOC sequestration.

The following hypotheses were formulated: (i) during the cover cropping phase, non-legume CCs reduce SMN and subsequent N_2O emissions relative to fallow by assimilating excess N in autumn; (ii) freezing of frost-sensitive CCs elevates SMN levels, leading to higher N_2O emissions during winter; and (iii) CCs with lower C:N ratios, which decompose more rapidly, result in

90   higher N_2O emissions after incorporation than those with higher C:N ratios; (iv) incorporation of CCs with greater biomass residues increases N_2O emissions in the following main crop; and (v) carbon inputs from above- and belowground biomass—and their contributions to SOC stocks—vary significantly among CC species.

2 Materials and methods

2.1 Study sites and experimental design

95   Field trials were conducted in central (Göttingen) and southern Germany (Ihinger Hof, Hohenheim), with replicated fields at each site, established in two consecutive years systematically named to reflect their location and establishment year. Specifically, the trials initiated in 2018 were labelled G18 for Göttingen and H18 for Hohenheim, while those initiated in 2019

were labelled G19 and H19, respectively. Each of these trials began in autumn and continued for approximately 18 months, with the 2018 trials ending in March 2020 and the 2019 trials in March 2021. Different fields were used at each site to avoid

100   residual effects between trials. The soils at both sites were classified as Luvisols (IUSS, 2015) with a pH of 7.0-7.5 (in 0.0125 M CaCl2). Details of soil characteristics and site information are presented in Table 1.

Table 1. Topsoil properties and site information for the different experimental trials.

Trial	Clay (%)	Silt (%)	Sand (%)	Organic C (%)	Bulk density (g cm^{-3})	Elevation (m a.s.l.)	Coordinates
G18	11.9	84.9	3.2	1.2	1.43	160	51°38'28.5"N 9°53'13.2"E
G19	14.3	70.9	14.8	1.4	1.50	150	51°28'22.3"N 9°54'52.7"E
H18	25.5	71.4	3.1	1.5	1.26	480	48°44'39.2"N 8°55'26.7"E
H19	28.3	69.7	2.0	1.2	1.29	483	48°44'42.9"N 8°55'25.5"E

Long-term climate data (1991-2020) from the German Meteorological Service (DWD, 2023) recorded average annual precipitation of 624 mm and temperature of 9.4°C for Göttingen, and 701 mm precipitation with a temperature of 9.1°C for

105   Hohenheim. Meteorological data, including daily precipitation and hourly soil and air temperatures, were collected from stations located at the field sites.

Field pea (*Pisum sativum* L.) was cultivated prior to the experiments due to its high residual soil Ncontent and potential for NO_3^- leaching (Voisin et al., 2002). Pea straw was left on the fields and incorporated into the soil by ploughing or deep rigid tine cultivator tillage. A randomized complete block design with four replications was set up at each site and year. Plot sizes

110   were 21x17 m in Göttingen and 30x19 m in Hohenheim, with sampling restricted to subplots of 2.7x14 m and 3x12 m, respectively. Three different CCs were sown in autumn: saia oat (*Avena strigosa* Schreb. var. "Pratex") and winter rye (*Secale cereale* L. var. "Traktor"), representing frost-sensitive and frost-tolerant grasses, respectively, and spring vetch (*Vicia sativa* L. var. "Mirabella"), a frost-sensitive leguminous CC. These were compared to a bare fallow during the CC cultivation period. The management details of the experimental trials are delineated in Table 2. Seedbed preparation was done using a disc or

115   rotary harrow. Seed rates were 120 kg ha^{-1} for rye, 80 kg ha^{-1} for oat, and 90 kg ha^{-1} for vetch, with row spacings of 12.5 cm in Göttingen and 15.0 cm in Hohenheim. During the CC phase, herbicides were applied in autumn for weed control in fallow plots and CC plots were not fertilized. In March of year following establishment, CCs were treated with glyphosate to terminate any plant growth after winter. To safeguard an optimal seedbed for sugar beet seedlings, rye was ploughed to a depth of 30 cm due to its extensive crown root and stem base material, while other treatments were tilled to 15 cm using a short disc harrow

120   or tine cultivator.

Sugar beet (*Beta vulgaris* L. var. "Lisanna") followed as the first main crop, sown at 45-50 cm row spacing and 90,000-95,000 plants ha^{-1} density. In accordance with the German fertilizer ordinance (German Fertilizer Ordinance, 2017), the N fertilization for sugar beet was adjusted to a total requirement of 180 kg N ha^{-1}. This total comprised the SMN measured in March in the 0-90 cm horizon and the mineral N applied thereafter. Detailed fertilization rates and application dates are provided in Table

125   2. Sugar beet following the rye treatment received an additional 100 kg N ha^{-1} due to a technical mistake. After harvest, sugar beet leaves were incorporated by 12-15 cm deep cultivator tillage before sowing winter wheat (*Triticum aestivum* var. "Nordkap") in October. Trials ended with the first N fertilization of winter wheat next March. Crop phases for the CCs and

sugar beet were defined from sowing to harvest, except for winter wheat, for which the crop phase ended at the first fertilization date.

Table 2. Management dates (YYYY-MM-DD) and N fertilizer rates for CC and main crop management across the experimental trials. *Rye treatment only.

	G18	G19	H18	H19
CC sowing	2018-08-29	2019-08-08	2018-09-12	2019-09-04
CC sampling	2018-11-19	2019-11-19	2018-12-06	2019-11-28
Glyphosate spraying	2019-03-15	2020-03-17	2019-03-22	2020-04-04
Soil tillage	2019-04-06	2020-04-01	2019-03-28	2020-04-09
Sugar beet sowing	2019-04-08	2020-04-03	2019-04-16	2020-04-16
N fertilizer application	2019-04-15	2020-09-04, (2020-06-12*)	2019-04-15, 2019-05-03	2020-04-15
N fertilizer amount (Kg N ha^{-1})	60	100, (100*)	130	140
Sugar beet harvest	2019-09-29	2020-10-01	2019-10-24	2020-09-28
Soil tillage/ ploughing	2019-09-30	2020-10-04	2019-10-29	2020-09-30
Winter wheat sowing	2019-09-30	2020-10-14	2019-10-30	2020-10-02
Winter wheat fertilization	2020-03-16	2021-03-15	2020-03-20	2021-03-11

2.2 Plant and soil sampling, analyses and calculations

The aboveground biomass of CCs was assessed by the end of November at each site-year using four sampling points within each plot, each covering an area of 0.5 m². To determine the dry matter (DM) content of the CC biomass, a subsample was mashed, and then dried at 60 °C for 48 hours. The resulting dry weight was then used to calculate the DM biomass. Elemental analysis was performed on the plant material to determine C and N concentrations, which were subsequently utilized to calculate the C and N contents of the aboveground CC biomass. Composite soil samples of five subsamples were taken biweekly from the topsoil (0-30 cm depth) using a 30 mm diameter auger. Samples were stored at -20°C until analysis. To determine SMN content (i.e. the sum of NO_3^- and NH_4^+), soil samples were extracted with 0.0125 M CaCl$_2$ solution in the ratio 1:4 (w/v) and analyzed according to VDLUFA A 6.1.4.1 (VDLUFA, 1991). Gravimetric water content was measured on subsamples dried at 105°C for 24 h. To determine soil bulk density, six undisturbed soil cores (250 cm³) per plot were taken in winter from the topsoil (3-8 cm, 13-18 cm and 23-28 cm), dried at 105°C for 24 h before weighing. Soil bulk density was calculated according to Eq. (1):

$$\rho b = \frac{Ms}{Vt},$$ (1)

Where ρb is the bulk density (g cm^{-3}), Ms is dry soil weight (g) and Vt is Soil volume (cm³).

Water-filled pore space was calculated from the gravimetric water content and the bulk density according to Eq. 2:

$$\text{WFPS} = \frac{\theta g * \rho b}{1 - \frac{\rho b}{\rho s}} * 100\%,$$ (2)

Where WFPS is the water-filled pore space (%), θg is the gravimetric water content (g g^{-1}), ρb is the bulk density (g cm^{-3}), ρs is the assumed particle density of 2.65 g cm^{-3} (Hillel, 2003).

2.3 Gas sampling and analysis

The closed chamber method was used for the N_2O flux measurements, with one chamber being placed per plot. Gas samples were taken weekly or more frequently after fertilization, high precipitation, or frost-thaw events. Two types of chambers were used at the study site in Göttingen: round chambers (60 cm diameter, 45 cm height) for the CC and winter wheat phases and rectangular chambers (72 cm length, 27 cm width, 18 cm height) for the sugar beet phase. Chambers were made of white opaque PVC and sealed with rubber straps or brackets. At the study site Hohenheim, gas fluxes were measured using chambers with an inner diameter of 30 cm as described in detail by Flessa et al., (1995). Four gas samples were taken from each chamber through a septum at 20 minute intervals. Samples were collected using a 30 mL syringe and stored in pre-evacuated 12 mL vials (Exetainer, Labco Limited, UK). At both study sites, laboratory analysis employed a SCION 456-GC gas chromatograph with an electron capture detector (ECD) for N_2O and a thermal conductivity detector (TCD) for CO_2. Samples were introduced using a Gilson auto sampler (Gilson Inc., Middleton, WI, USA). Data processing was performed using '*CompassCDS*' software. The analytical precision of the gas chromatograph was determined monthly by repeated measurements using certified standard gases (307, 760, and 6110 ppb for N_2O, and 201, 550, and 2500 ppm for CO_2).The coefficient of variation was consistently $< 2\%$. Mass concentrations were calculated from molar concentrations using the ideal gas equation considering the chamber temperature.

Flux rates were calculated using the "*gasfluxes*" R package (Fuss and Hueppi, 2020), selecting models based on the Akaike information criterion and Kappa value. Cumulative N_2O emissions for the different cropping phases were estimated using "*aggfluxes*" function with linear interpolation between measurement dates and summed to result in the cumulative fluxes of the entire trials. Potentially mitigated indirect N_2O emissions were estimated by multiplying the late autumn N uptake of CC shoots by the IPCC (2019) factors: the N_2O emission factor for indirect emissions due to N leaching and runoff ($EF_5 = 0.011$ kg N_2O-N per kg N) and the factor for N losses by leaching and runoff in wet climates ($Frac_{LEACH} = 0.24$ kg N per kg N). CO_2 equivalents (CO_2-eq) were calculated by using the N_2O global warming potential of 273 (IPCC, 2022).

2.4 Data and statistical analyses

Data processing and analyses were carried out in R version 4.2.2 (R Core Team, 2023). For all statistical analyses, the significance level was set to $p<0.05$. N_2O fluxes and cumulative emissions were $\log_{10}$ transformed to ensure normal distribution and variance homogeneity of model residual. Variance homogeneity and approximate normality of residuals was assessed using diagnostic plots. Flux rates that were strongly negative (i.e. lower than -60 g N_2O-N ha^{-1} d^{-1}) as well as those with standard errors larger than 120 µg N_2O-N m^{-2} h^{-1}, indicating high uncertainty, were excluded. In addressing the discrepancy in fertilizer application in the G19 trial, data from rye treatment, which had received the double fertilizer dose, were included in analyses, plots and tables specific to individual site-year evaluations. However, for comprehensive analyses that combined data across all site-years, the rye treatment data from G19 during the sugar beet and winter wheat phases were excluded to maintain consistency and comparability across the study. ANOVA was performed on linear models for treatment differences,

with Tukey HSD tests for post-hoc comparisons. A generalized least-squares regression model assessed CC impact on cumulative N_2O emissions, average SMN and WFPS across site-years, using the *'nlme'* package (Pinheiro et al., 2023). Variance heterogeneity was addressed using the variance structure $\sigma^2 \times |y|^2 \delta$ (Zuur et al., 2009), applied when found significant.

185 Upon identifying a significant CC treatment effect via ANOVA, pairwise mean comparisons, with Tukey-adjusted p-values, were performed on the estimated marginal means through the *'emmeans'* package (Lenth et al., 2023). The impact of environmental variables on N_2O flux was analyzed using linear mixed-effects models with '*lmer*' function from '*lme4*' package (Bates et al., 2015). To ensure comparability and address differences in scale, predictors were standardized using Z-score normalization from the 'scales' package (Wickham et al., 2023). Biweekly SMN and WFPS values were linearly interpolated

190 to match the weekly N_2O flux measurements. The models included standardized SMN, WFPS, soil temperature, and CC treatments as fixed effects, while site-year was incorporated as a random effect to account for variability across different sites and years.

2.5 Modelling changes in SOC stocks

The effect of CCs on SOC sequestration in a 30 cm topsoil horizon was simulated over a period of 50 years for two different

195 crop rotations, common in German agricultural practice. Crop rotation CR1, with a CC embedded every second year, had the sequence CC/bare fallow – sugar beet – winter wheat – CC/bare fallow – silage maize – winter wheat with an application of 30 m^3 digestate from biogas plants before seeding of maize. Crop rotation CR2 had the crop sequence CC/bare fallow – sugar beet - winter wheat – winter rape – winter wheat, with a CC in every 4th year. No organic fertilizer was applied in crop rotation CR2. For both crop rotations CR1 and CR2, a control without any CC was defined in contrast to 3 CC scenarios with saia oat,

200 spring vetch and winter rye as CC. In the control and CC scenarios, it was assumed that the above-ground crop residues for winter wheat, sugar beet and winter oilseed rape remained in the field. Effects of CCs were quantified by subtracting modelled C stocks of the control (bare fallow instead of CC) from modelled C stocks of CC treatments. Because the models RothC and C-Tool describe soil C decomposition by first order kinetics, modelled SOC change between scenarios is linearly dependent on differences in initial C stocks and C inputs between control and CC scenarios, meaning that in our setup frequency and

205 biomass production of grown CCs mainly control modelled effects on SOC stocks.

The long-term potential for changes in SOC content due to the cultivation of CCs was estimated using a model ensemble (Seitz et al., 2023) consisting of the RothC (Coleman and Jenkinson, 1996) and C-Tool (Taghizadeh-Toosi et al., 2014) models implemented in R using the SoilR package (Sierra et al., 2012) in combination with three allometric functions for calculating the C input from shoot and root residues of main crops in dependence on yields (Franko et al., 2011; Jacobs et al., 2020;

210 Rösemann et al., 2021). If no yield information was available for main crops, documented yields from German agricultural soil inventory sites (Jacobs et al., 2020) within a radius of 50 km were used and averaged. Yields of main crops after the CC (CC scenarios) or after the alternative bare fallow period (control) were based on observed yields from experimental treatments where the main crops followed the same CCs (saia oat, spring vetch, or winter rye) or bare fallow treatment. The C inputs of the CCs were taken from measured aboveground biomass (experimental data) and root-shoot ratios, which in turn were derived

215 based on measurements of above- and belowground biomass of the CCs grown at the Göttingen site. In order to derive the C input for root biomass from CCs for the horizon of interest of 0-30 cm profile depth, an approach according to Gale and Grigal (1987) was used to describe the root distribution as a function of depth:

$$Y = 1 - \beta^d \quad (3)$$

Here, Y is the root fraction increasing with depth, β is a parameter and d is the depth of the profile in cm. Jackson et al. (1996)
220 set β = 0.961 to describe the depth distribution of roots of cropland crops (Jackson For CCs, plant-specific values of β were determined via calibration on the basis of plant-specific available data on below-ground biomass at the Göttingen site (Figure S1, Supplementary Table S6). Estimated proportion of roots in the 0-30 cm depth profile was higher for winter rye (89 %) than for saia oat and spring vetch (79% each). In relation to the profile depth of 0-30 cm considered here, this resulted in root-to-shoot ratios of 0.24, 0.13 and 0.33 for saia oat, spring vetch and winter rye, respectively. It was assumed that C input from root
225 exudates corresponded to 31% of the input from root C according to Jacobs et al. (2020).

Weather data with a monthly resolution for precipitation, temperature, and global radiation (2018-2021) were obtained from DWD grid data, as it aligns with the experimental crop growth periods at both sites. The suitability of this data has been validated in model evaluation studies for SOC models at German permanent observation sites (Riggers et al., 2019). To match the 50-year simulation period, these time series were repeated. Model initialization was performed separately for each model
230 in the ensemble. For RothC, pool distribution at equilibrium was determined using an analytical solution (Dechow et al., 2019), while for C-Tool, the initial pool fractions followed the approach proposed by Taghizadeh-Toosi et al. (2014).

3 Results and Discussion

3.1 Weather conditions and effect of CCs on soil WFPS

The experimental trials experienced marginally warmer and drier conditions in the first establishment year compared to long-
235 term averages (Table 3). In 2018, the rainfall totals in Göttingen and Hohenheim were 430 mm and 526 mm, respectively. The temperature ranges were from -5 to 30 °C, with occasional extremes, such as a cold spell in mid-February 2021. Soil temperatures generally fluctuated between 0 and 25°C, although several frost events were recorded at a 5-cm depth (Figure 1). Water-filled pore space exhibited a consistent seasonal pattern across all site-years, starting low in autumn, increasing through winter to peak around February, and declining in spring and summer, with occasional short-term spikes following heavy
240 summer rainfall (Figure 1, Table 3).

Table 3. Weather conditions and soil water filled pore space (WFPS) across different cropping phases and site-years. Means ± (SD). Different lowercase letters indicate statistically significant differences between site-years within each column (p<0.05).

	Cover crop phase	Sugar beet phase	Winter wheat phase	Entire trial
Mean temperature [°C]				
G18	7.1 (5.6)	16.1 (5.2)	6.1 (4.2)	9.6 (6.7)
H18	5.4 (5.4)	14.8 (4.8)	3.8 (3.5)	8.3 (6.8)
G19	8.1 (6)	15.6 (4.3)	4.1 (5.8)	9.5 (7.1)
H19	6.2 (5)	15.7 (4.1)	3.9 (5.1)	8.4 (6.8)
Mean weekly precipitation [mm week^{-1}]				
G18	13.3 (14.7)	11 (12.4)	16.6 (12)	13.6 (13.3)
H18	9.1 (9.8)	13.9 (14.4)	10.5 (8.5)	11.2 (11.5)
G19	17.7 (18.9)	16.4 (21.1)	7.5 (6.9)	14.6 (17.8)
H19	9.7 (8.1)	11 (12.7)	6.9 (7.7)	9.3 (9.6)
Soil moisture [%WFPS]				
G18	57 (24) a	54 (20) a	79 (16) a	62 (24) a
H18	66 (23) b	47 (14) b	71 (9) b	62 (21) a
G19	65 (20) b	47 (14) b	70 (11) bc	61 (19) a
H19	75 (12) c	54 (13) a	69 (12) c	67 (15) b

245 **Table 4.** Dry matter biomass (DM), carbon (C) and nitrogen (N) contents, and C:N ratio of winter CCs in late autumn across site-years. Means (n=4 for individual trials, n=16 for averages across all site-years) ±(SD). Significant differences between CC species within each category are denoted by different lowercase letters (p<0.05).

	G18	H18	G19	H19	Mean
DM (t ha^{-1})					
Winter rye	4.4 (0.2) a	2.7 (0.4)	3.5 (0.2) a	4.3 (0.5) a	3.6 (0.8) a
Saia oat	3.8 (0.2) b	2.6 (0.6)	2.1 (0.3) b	2.3 (0.3) b	2.7 (0.8) a
Spring vetch	1.9 (0) c	2.7 (1.9)	2.4 (0.3) b	1.9 (0.6) b	2.2 (0.7) b
C content (t C ha^{-1})					
Winter rye	1.2 (0.1) a	1.1 (0.1) a	1 (0.1) a	1.7 (0.2) a	1.2 (0.2) a
Saia oat	1.1 (0.1) a	0.9 (0.1) a	0.7 (0.1) b	1 (0.1) b	0.9 (0.2) b
Spring vetch	0.7 (0) b	0.4 (0) b	0.9 (0.1) ab	0.7 (0.2) b	0.7 (0.2) c
N content (kg N ha^{-1})					
Winter rye	109 (9) a	64 (12)	99 (2) a	172 (9) a	103 (37) a
Saia oat	104 (5) a	61 (11)	50 (4) b	82 (10) b	75 (23) b
Spring vetch	77 (1) b	41 (3)	92 (11) a	78 (22) b	76 (21) ab
C:N ratio (-)					
Winter rye	11 (0.7) a	17.1 (0.9) a	10.4 (0.5) a	9.6 (0.6) a	12.5 (3.2) a
Saia oat	10.9 (0.6) a	15.7 (0.9) a	13.6 (0.8) b	11.7 (0.5) b	12.8 (1.9) a
Spring vetch	8.6 (0.4) b	8.8 (0.4) b	9.6 (0.4) a	8.4 (0.1) a	8.9 (0.6) b

Concerns have been raised about the potential for increased evapotranspiration from CCs to adversely impact soil moisture

250 (Unger and Vigil, 1998). In the G18 trial, WFPS under CC treatments was marginally lower than in fallow plots during the cover-cropping phase, though these differences were not statistically significant (Supplementary Table S1). The lower soil moisture observed in CC plots in G18, likely reflecting the reduced rainfall of 430 mm, supports concerns that increased evapotranspiration from CCs in semi-arid conditions (annual rainfall typically 250-500 mm) or in drier-than-average temperate years may reduce soil moisture and potentially affect subsequent crop yield (Blanco-Canqui et al., 2015; Mitchell et al., 2015).

255 However, studies (Wang et al., 2021; Qi et al., 2011) indicate that the impact of CCs on pre-sowing soil moisture, water storage

potential, and yield is highly site-specific, and any negative effects on topsoil moisture may be offset by enhanced water holding capacity resulting from increased soil organic matter (Poeplau and Don, 2015). Indeed, long-term use of CCs such as rye has been shown to significantly improve field capacity and plant-available water (Basche et al., 2016).

3.2 Influence of CC species on SMN dynamics

260 Soil mineral N was predominantly composed of NO_3^-, with ammonium (NH_4^+) levels remaining below 10 kg N ha^{-1} on most sampling dates. At the onset of trials, SMN levels varied among sites and years, with the highest average in G18 (80±20 kg N ha^{-1}), followed by G19 (48±14 kg N ha^{-1}) and the lowest in Hohenheim (29±8 and 33±9 kg N ha^{-1} for H18 and H19, respectively). No significant differences in initial SMN levels were found between treatments within each trial (Figure 1, Table S2).

265 In the present study, the cultivation of field pea as the preceding main crop led to elevated SMN levels in late summer, which were substantially higher in Göttingen than in Hohenheim. Subsequently, we observed an increase in SMN across all treatments and site-years for a few weeks following the incorporation of pea straw (see Fig. 1). This trend can be attributed to the net mineralization of the pea residues, a common characteristic of legumes with low C:N ratios that promote swift decomposition and N release (Doran and Smith, 1991).

270 By late autumn, significant differences in aboveground biomass DM were observed across all site-years (except H18), with rye consistently achieving higher DM (3.6 t ha^{-1}) than oat and vetch (2.7 and 2.2 t ha^{-1}, respectively; Table 4). Correspondingly, rye exhibited the highest aboveground C content (1.2 t ha^{-1}) and N uptake (103 kg N ha^{-1}), while oat and vetch showed lower values (0.9 and 0.7 t ha^{-1} for C content, and 75 and 76 kg N ha^{-1} for N uptake, respectively). The C:N ratio of CC shoot biomass was consistently lower for vetch (<10) compared to rye and oat (Table 4). Simultaneously, SMN levels in CC treatments

275 gradually declined during autumn while remaining elevated in fallow plots, with the decline being most pronounced for rye. By the end of the CC growing period in late November, all CC treatments exhibited significantly lower SMN than fallow across all site-years (Figure 1, Table S2). In G18, the SMN difference between rye and fallow was approximately 130 kg N ha^{-1}, 80 kg N ha^{-1} in G19, and about 30 kg N ha^{-1} in both H18 and H19. Among the evaluated CCs, rye was most effective in reducing SMN—likely due to its higher biomass production, robust N uptake, and frost resilience. This observation aligns

280 with finings of Thapa et al. (2018), who reported a positive correlation between CC biomass and NO_3^- uptake. In Göttingen, the more pronounced SMN differences likely reflect the higher initial SMN compared to Hohenheim. In H18, Koch et al. (2022) found that the SMN difference across the 0-90 cm soil profile closely matched the N content in rye shoots, whereas in H19, rye shoot N exceeded the SMN difference, underscoring rye's efficient N uptake and its role in mitigating NO_3^- leaching. Conversely, in Göttingen (G18 and G19), rye shoot N accounted for only about half of the SMN difference, suggesting

285 contributions from unquantified factors such as root biomass, exudates, and N immobilization. Additionally, vetch was the least effective in reducing SMN, likely due to its shallower root system (Grunwald et al., 2022) and its capacity for biological N fixation (Ramirez-Garcia et al., 2015), with winter legume CCs generally producing less biomass than summer legumes and thus exerting a diminished impact on soil N uptake (Pan et al. 2022).

From November through January, SMN levels declined consistently across all treatments, reaching their lowest values in
290 January (27 ± 12 kg N ha^{-1} in Göttingen and 8 ± 6 kg N ha^{-1} in Hohenheim; Figure 1). This decline was most pronounced in fallow plots, which began with the highest SMN levels in November. While part of the winter decrease in SMN may result from NO$_3^-$ leaching beyond the topsoil, the present study did not assess the entire root zone. Nonetheless, previous research has shown that CC cultivation can reduce NO$_3^-$ leaching by approximately 68% compared to fallow (Lapierre et al., 2022; Nouri et al., 2022), highlighting the significant role of CCs in enhancing N retention.

295 Following the frost event in late January 2019, a notable increase in SMN was observed in the frost-sensitive oat and vetch treatments in G18, as well as in oat in H18 (Figure 1a). By the end of the cover cropping phase in April, plots with rye exhibited the lowest SMN levels (Figure 1, Table S2), although the differences were not statistically significant in most site-years. Across all site-years, average SMN values during the cover-cropping phase were lowest for non-legume CCs (rye and oat) and highest for bare fallow (Figure 2a), with rye exhibiting significantly lower SMN than fallow in every trial (Supplementary
300 Table S3). This confirms the first part of hypothesis (i), demonstrating that during the cover cropping phase, non-legume CCs reduce SMN by assimilating excess N in autumn. In contrast, vetch did not consistently reduce SMN—a finding that aligns with previous research suggesting that legumes, through their capacity for atmospheric N fixation, rely less on soil N uptake (Daryanto et al., 2018; Helfrich et al., 2024; Ramirez-Garcia et al., 2015).

Subsequent to the incorporation of CC residue, sugar beet sowing, and N fertilization in April, SMN levels increased to 111-
305 247 kg N ha^{-1} at the onset of the sugar beet phase, effectively masking differences among CC treatments. As sugar beet N uptake increased, SMN levels declined strongly between June and July, reaching their lowest values around September (Figure 1, Table S2). Subsequent N fertilization—in G19 for the rye treatment and across all treatments in H18—elevated SMN levels, yet no significant differences among CC treatments were observed during the sugar beet phase (Figure 2), suggesting that within a fertilized framework the effect of winter CCs on SMN becomes negligible. Subsequent to the sugar beet harvest, soil
310 cultivation, leaf residue incorporation, and winter wheat sowing, a notable SMN increase was observed across all site-years, with higher levels recorded in Göttingen compared to Hohenheim (Figure 1, Table S3). Over the course of the entire trial, average SMN levels were highest in G18, intermediate in G19, and lowest in both H18 and H19 (Table S3). Non-legume CC treatments resulted in significantly lower SMN than bare fallow, with the rye treatment exhibiting the lowest average SMN (Figure 2, Table S3). These findings underscore the notion that N fertilization can supersede the impact of winter CCs on
315 SMN. However, in settings devoid of fertilization, CCs may exert a more pronounced influence on regulating soil N availability and yield (Koch et al., 2022; Kühling et al., 2023).
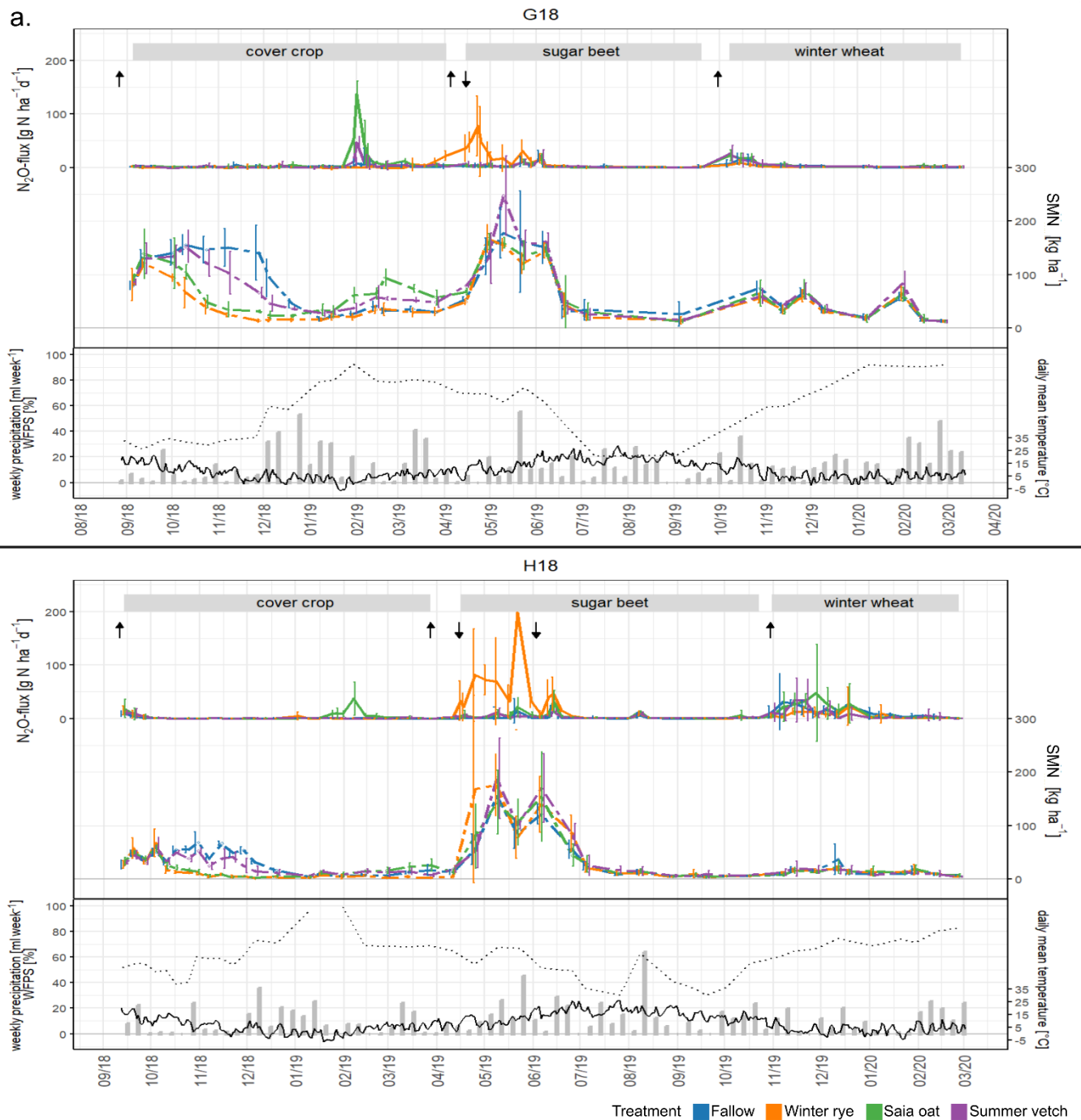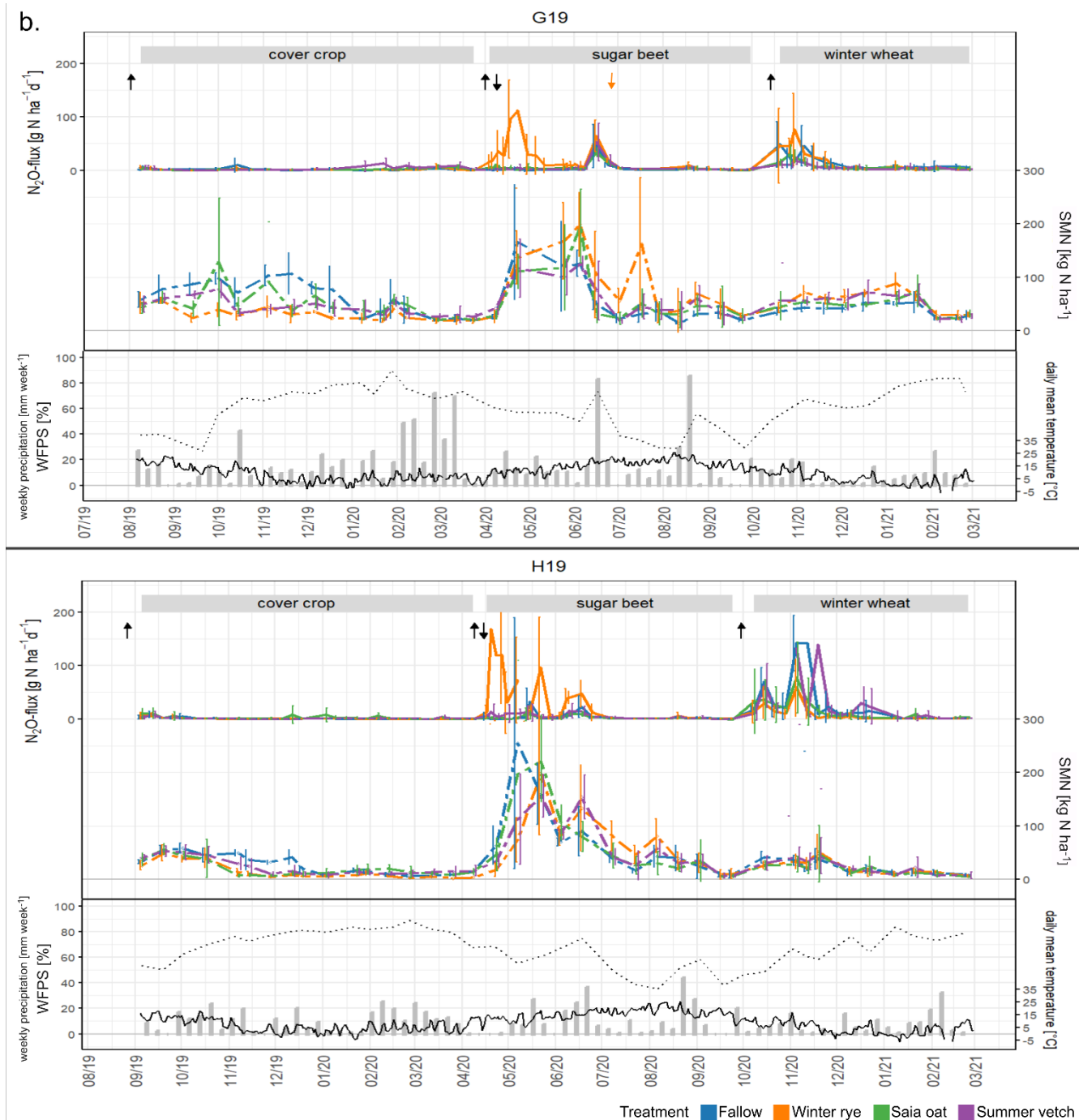
Figure 1. Dynamics of N₂O flux rates and soil mineral nitrogen (SMN) contents, presented as mean ± SD (n=4). Seasonal changes in topsoil water-filled pore space (WFPS%, dotted black line), daily mean air temperature (continuous black line) and weekly precipitation (gray bars) for Göttingen (upper plot) and Hohenheim (lower plot) throughout the different cropping phases for various CC treatments in (a) 2018 trials and (b) 2019 trials. Upward arrows mark soil cultivation events, while downward arrows signify N fertilization of sugar beets.

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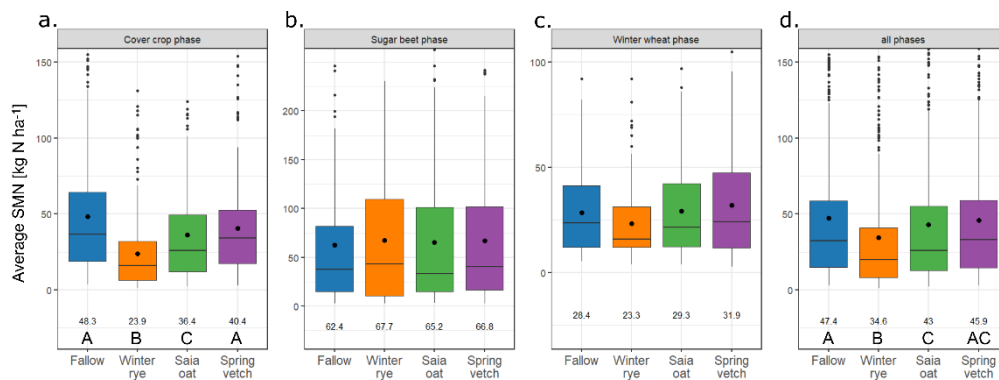


Figure 2. Mean soil mineral nitrogen (SMN) during the different cropping phases (n=12 for rye treatment in the sugar beet, winter wheat and all phases together, n=16 for all other treatments). Horizontal lines represent the median, large dots and numbers at the bottom show the mean. Uppercase letters indicate significant differences of Z-standardized Nmin values between the treatments (p<0.05).

3.3 Influence of CC species on N_2O flux rates and cumulative N_2O emissions

330 Across all site-years, spatial and temporal variations in N_2O flux rates were observed, with heavy rainfall and elevated WFPS frequently triggering emission peaks (Figure 1). The availability of SMN in the forms of NH_4^+ and NO_3^- (which serve as substrates for nitrification and denitrification) and appropriate soil moisture and temperatures that promote microbial activity are crucial factors influencing N_2O production in agricultural soils (Signor and Cerri, 2013). Although the initial weeks of the trials exhibited elevated SMN levels and adequately warm soil temperatures, high N_2O flux rates were not observed, a

335 discrepancy likely due to the low WFPS recorded during late summer (Signor and Cerri, 2013). This observation is consistent with the findings of Cosentino et al. (2013), who posited that WFPS values below 59% impede N_2O production. While Smith et al. (2003) observed an increase in N_2O flux rates with rising WFPS, suggesting that when SMN is not a limiting factor, N_2O production is enhanced. Throughout the cover cropping phase, N_2O flux rates remained relatively low, a phenomenon attributed to suboptimal microbial conditions during autumn and winter—specifically reduced temperatures and limited

340 availability of C and N. Cosentino et al. (2013) emphasized that soil temperatures below 14°C suppress N_2O emissions, and Rummel et al. (2021) demonstrated that increased soil moisture does not boost N_2O emissions when NO_3^- is limited. An added benefit of cultivating frost-sensitive CCs is their natural termination under appropriate winter conditions, which eliminates the need for chemical termination via herbicides. However, the termination stage significantly influences the mineralization rate of plant residues and their potential to promote N_2O emissions, with immature residues leading to higher emissions (Abalos et

345 al., 2022). In the present study, following a frost event in late January 2019, frost-sensitive oat treatments in G18 and H18 exhibited pronounced N_2O emission peaks, reaching 137 (±24) g N_2O-N ha^{-1} d^{-1} in G18, with a smaller yet significant peak observed in the vetch treatment in G18. The more severe and prolonged frost in G18 resulted in greater damage to CCs in Göttingen, subsequently leading to higher N_2O emission peaks. These findings are consistent with those reported by Wagner-

Riddle et al. (2017) who found that cumulative annual N_2O emissions in cold regions are closely linked to the number of freezing-degree days. This highlights the critical impact of temperature dynamics on N_2O emissions.

The increase in N_2O emissions from frost-sensitive CCs during winter can be attributed to the degradation of frost-damaged organic matter. This organic matter undergoes accelerated microbial decomposition, increases N availability, and promotes microbial respiration. These processes may create anoxic microsites favorable for N_2O production (Beauchamp et al. 1989; Chen et al. 2013; Kravchenko et al., 2017). However, during milder winters, such as observed in the H19 trial, CCs persisted through the season, leading to no notable differences in cumulative N_2O emissions among the treatments during the cover-cropping phase (Supplementary Table S4). This suggests that without early frost termination, frost-sensitive CCs share comparable effects on N_2O emissions with their frost-resistant counterparts. This observation aligns with the findings of Storr et al. (2021), who determined that frost-sensitive CC species may not always terminate under temperate climates, but they continue to provide a steady supply of available C and N as the plants senesce.

During the cover-cropping phase, the frost-sensitive oat treatment resulted in higher cumulative N_2O emissions compared to other treatments in three out of four site-years, with this difference reaching statistical significance in both 2018 trials (G18 and H18). While vetch recorded the highest cumulative emissions in G19 (Supplementary Table S4). When data were combined across all site-years, treatments involving frost-sensitive CCs—particularly oat—exhibited significantly higher cumulative N_2O emissions compared to bare fallow (Figure 3). These results confirm hypothesis (ii), indicating that frost-induced damage in sensitive CCs leads to increased N_2O emissions. Despite non-legume CCs reducing SMN levels relative to fallow during the cover cropping phase, their cumulative N_2O emissions did not decrease accordingly. This finding suggests that SMN concentration alone does not govern N_2O emissions; instead, a combination of factors, including temperature, water-filled pore space, and the availability of C and N, plays a critical role. Consequently, this outcome does not fully support hypothesis (i), which posited that non-legume CCs reduce SMN—and subsequent N_2O emissions—relative to fallow by assimilating excess N in autumn.

In our comparison of cumulative N_2O emissions from frost-sensitive CCs, we found that our initial hypothesis (iii)—that residues with lower C:N ratios cause higher N_2O emissions—was not supported. Instead, the C and N contents, which correlated with the DM of the residues, emerged as a more reliable indicator in this study. Despite oat having significantly higher C:N ratios than vetch, it still induced higher cumulative N_2O emissions when its C and N contents were higher (Table 4, Supplementary Table S4). Moreover, although differences in C:N ratios existed between oat and vetch, both fell within a range known to facilitate net mineralization and increase soil NO_3^- content thereby promoting N_2O losses (Li et al., 2013). This observation aligns with the findings of Millar and Baggs (2004) and Li et al. (2013), indicating that a greater release of readily available C and N from residues with similar C:N ratios results in increased microbial activity and consequently, higher N_2O emissions.

A substantial body of research has documented a rapid increase in N_2O emissions following N fertilizer application, primarily due to enhanced substrate availability for nitrification and denitrification (Dobbie and Smith, 2003; Weitz et al., 2001). Similarly, the addition of organic amendments to improve soil fertility and crop productivity can stimulate N_2O emissions

through mechanisms such as the priming effect (Thangarajan et al., 2013). The incorporation of CC residues has also been linked to significant increases in N_2O emissions (Abalos et al., 2022). with Mutegi et al. (2010) attributing 60% of annual N_2O emissions to tillage and residue incorporation. In this study, the incorporation of CC residues combined with sugar beet sowing and N fertilization resulted in elevated N_2O flux rates lasting six to eight weeks across all treatments. Interestingly, despite comparable SMN levels across treatments due to N fertilization, the rye treatment exhibited significantly higher cumulative N_2O emissions during the sugar beet phase (3.4 kg N_2O-N ha^{-1}) compared to fallow, oat, and vetch (approximately 0.5-0.66 kg N_2O-N ha^{-1}). These results support hypothesis (iv), demonstrating that incorporating CC residues with higher biomass leads to increased N_2O emissions. Unlike the shallow tilling (15 cm) applied in most treatments, rye required deep ploughing (up to 30 cm) to manage its extensive root system, which may have further influenced N_2O emissions by disturbing soil organic biomass and enhancing mineralization rates. Observations from the Göttingen trials suggest that variations in incorporated CC biomass are the primary drivers behind these differences; the larger biomass of fresh rye residues likely resulted in increased C turnover, heightened microbial activity, more rapid oxygen depletion, and the formation of anaerobic microsites that favored N_2O production (Blagodatsky et al., 2011). Additionally, WFPS exerted a notable influence on N_2O flux rates during the sugar beet phase (Supplementary table S5), with increased emissions observed following heavy rainfall events. While subsequent N fertilization in the rye treatment (in G19) and across all treatments in H18 raised SMN levels, N_2O flux rates were much lower later in the season when WFPS had declined. From July until the end of the sugar beet phase, N_2O flux rates nearly diminished to non-detectable levels, likely reflecting reduced WFPS and minimal SMN as a result of robust N uptake by the maturing sugar beet plants. According to the IPCC emissions factor for wet climates, approximately 0.6% of the N present in crop residues is converted into N_2O (IPCC, 2019). For rye, with an average shoot biomass N content of 103 kg N ha^{-1}, this conversion would account for only about 21% of the observed 2.9 kg N_2O-N ha^{-1} increase compared to fallow during the sugar beet phase. Thus, additional contributions from rye root decomposition and enhanced soil organic matter decomposition likely explain the surplus N_2O emissions. Li et al. (2015) observed that residues with high C:N ratios can still lead to significant N_2O emissions if the C is readily decomposable, while Abalos et al. (2022) identified N and easily degradable organic fractions as key factors affecting N_2O emissions from crop residues. Therefore, the elevated cumulative N_2O emissions following rye incorporation can be attributed to its high biomass yield and the large amounts of readily decomposable C and N from its residues.

After the sugar beet harvest, subsequent soil cultivation, leaf residue incorporation, and winter wheat sowing led to an increase in N_2O fluxes. During the winter wheat phase, cumulative N_2O emissions were significantly lower in the rye treatment than in the fallow and vetch treatments, even though no residual effect of the CCs on SMN levels was observed. Furthermore, SMN levels had a significant effect on N_2O fluxes during the winter wheat phase (Supplementary Table S5), indicating that SMN might have been the limiting factor for N_2O production in this phase.

The majority of studies investigating CCs in agricultural rotations have focused on short-term N_2O emissions during either CC growth or following residue incorporation, leaving a knowledge gap regarding year-round N_2O emissions in systems incorporating CC cultivation (Muhammad et al., 2019). In the current study, even though non-legume CCs consistently

produced lower SMN values than bare fallow over the entire trial period—with rye showing the lowest SMN levels—rye resulted in the highest total cumulative N₂O emissions, followed by oat and vetch, while fallow exhibited the lowest emissions. Nevertheless, these differences were not statistically significant over the entire trial period. These findings are consistent with

420 those of Basche et al. (2014), who reported that CCs tend to have a net neutral effect on N₂O emissions when measured over long periods, highlighting the importance of long-term measurements to better understand the full impact of CCs on N₂O dynamics.

Despite higher SMN levels in Göttingen, cumulative N₂O emissions over the entire trial were generally greater in the Hohenheim trials—highest in H19 and lowest in G18—although these differences were not statistically significant (Table S4).

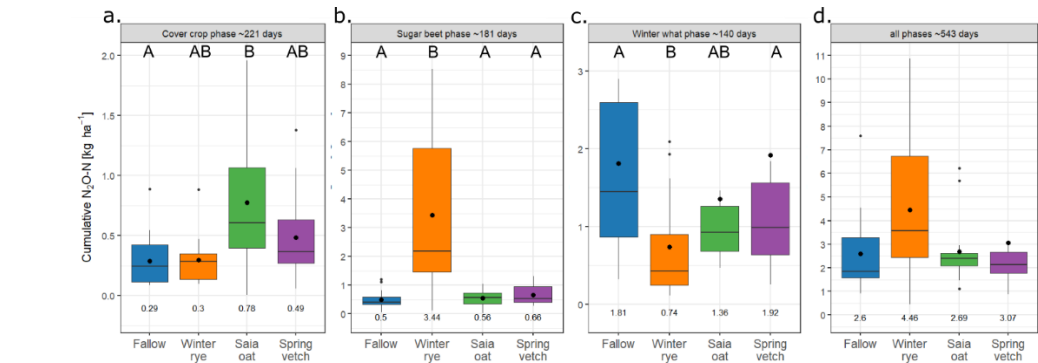
425 This discrepancy may be attributed to the higher clay content in Hohenheim soils, which likely reduced gas diffusivity, promoted the formation of anaerobic microsites, and consequently elevated denitrification rates—a factor known to increase N₂O emissions (Bollmann and Conrad, 1998; Pelster et al., 2012). These findings underscore the importance of soil type and climatic conditions in regulating N₂O emissions.

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Figure 3. Cumulative N₂O emissions across the different cropping phases. Mean ± SD (n=12 for rye in sugar beet and winter wheat phases and all phases combined; n=16 for all other treatments). Horizontal lines represent the median, large dots and numbers at the bottom show the mean. Uppercase letters indicate significant differences of Z-standardized cumulative N₂O emission values between the treatments (p<0.05).

435 **3.4 Mitigation potential of indirect N₂O emissions by non-legume CCs**

The mitigation potential for indirect N₂O emissions induced by NO₃⁻ leaching—calculated from non-legume CC N uptake in late autumn—was significantly higher in rye, averaging 0.27 kg N₂O-N ha⁻¹ a⁻¹ (approximately 116 kg CO₂-eq ha⁻¹ a⁻¹). Oat reduced emissions by an average of 0.2 kg N₂O-N ha⁻¹ a⁻¹ (approximately 85 kg CO₂-eq ha⁻¹ a⁻¹ ; Table 5). It should be noted that vetch was excluded from the calculation due to uncertainties in distinguishing soil N uptake from N biologically fixed.

440 The cultivation of CCs, particularly during periods of high soil N availability and precipitation, has been demonstrated to absorb excess N, and thereby reduce NO₃⁻ leaching, mitigating indirect N₂O emissions. Although CC cultivation in this study did not diminish direct N₂O emissions—and, in the case of rye, slightly increased them—the observed potential reduction in NO₃⁻ leaching suggests a potential to lower indirect N₂O emissions. This finding is in line with Parkin et al. (2016), who reported that rye, while neutral regarding direct N₂O emissions, substantially decreased indirect N₂O emissions over a decade-

445 long trial. However, the methodology employed here, based on N content in CC above-ground biomass, provides an approximate estimate of the potential mitigation of indirect N_2O emissions. It does not account for soil water movement, N concentrations in leachate, N stored in roots the nor the N mineralization occurring during the winter period. Furthermore, mitigation levels likely vary with soil type and climatic factors, with sandy soils and periods of high precipitation exhibiting more pronounced effects (Simmelsgaard, 1998). Thus, these results represent an oversimplification of the complex processes

450 involved and should be interpreted with caution.

Table 5. Mitigation potential of non-legume cover crops (CCs) in reducing indirect N_2O emissions induced by N leaching derived from pre-winter N uptake of CCs. Mean values (n=4 for individual trials, n=16 for overall averages) ± (SD). Statistically significant differences between rye and oat within each trial and overall averages are denoted by different lowercase letters.

		Mitigation potential	
		kg N_2O-N ha^{-1} a^{-1}	kg $CO_{2\text{-eq}}$ ha^{-1} a^{-1}
G18	Winter rye	0.29 (0.02)	123 (10)
	Saia oat	0.28 (0.01)	118 (6)
H18	Winter rye	0.17 (0.03)	73 (14)
	Saia oat	0.16 (0.03)	69 (12)
G19	Winter rye	0.26 (0.01) a	112 (3) a
	Saia oat	0.13 (0.01) b	57 (5) b
H19	Winter rye	0.45 (0.02) a	194 (10) a
	Saia oat	0.22 (0.03) b	93 (11) b
Mean	Winter rye	0.27 (0.1) a	116 (42) a
	Saia oat	0.2 (0.06) b	85 (26) b

3.5 Effect of CCs on long-term soil C sequestration

455 According to our model results, soil C sequestration from winter rye, saia oat and spring vetch significantly contributes to greenhouse gas mitigation by CCs and is a relevant sink compared to direct and indirect N_2O fluxes. At the Göttingen sites, average C inputs from main crops in the control scenarios (no CC) were about 4.15 and 4.51 t C ha^{-1} a^{-1} for crop rotations CR1 and CR2, respectively, whereas at the Hohenheim site they were approximately 10% lower (3.76 and 4.15 t C ha^{-1} a^{-1}; Supplementary Table S7). CR1 exhibited lower C inputs than CR2, primarily due to a higher share of winter crops that maintain

460 larger amounts of incorporated residues, even though CCs were grown at a two-year interval in CR1 compared to every four years in CR2. Among the CCs, winter rye exhibited the highest C inputs, providing additional increases of 20-24% in CR1 and 9-11% in CR2. Saia oat followed, with increases of 15-17% in CR1 and 7-8% in CR2, and spring vetch had the lowest increases, with 11-12% in CR1 and 5% in CR2 (Supplementary Table S8). As anticipated, the rate of C sequestration was observed to be approximately double that of the four-year cultivation interval (CR2) in the two-year cultivation interval (CR1).

465 In CR1, the annual C sequestration rates averaged for the simulation periods of 50 years were highest for winter rye (0.13 and 0.15 t C ha^{-1} a^{-1} for Göttingen Hohenheim, respectively), followed by saia oat (0.11 and 0.12 t C ha^{-1} a^{-1} for Göttingen and Hohenheim, respectively) and spring vetch (0.09 t C ha^{-1} a^{-1} for both sites, Table 6). Sequestration rates found here for a 30-cm profile are of the same order or slightly lower than those reported in several meta-studies (Abdalla et al., 2019; Blanco-

Canqui, 2022; Bolinder et al., 2020; Poeplau and Don, 2015). For example, Poeplau and Don (2015) reported an averaged

470   sequestration rate of 0.32±0.08 Mg C ha^{-1} a^{-1} in the 0-22 cm depth interval. Assuming proportionality between C input and

soil C stock changes and a uniform SOC distribution in the plow horizon, this would translate to sequestration rates of 0.21 ±

0.05 Mg C ha^{-1} a^{-1} for a cover crop grown every second year and 0.11 ± 0.04 Mg C ha^{-1} a^{-1} for one grown every fourth year.

These CC related effects are higher than those obtained in our modeling study (0.09-0.15 Mg C ha^{-1} a^{-1} for CR1 and 0.05-0.08

Mg C ha^{-1} a^{-1} for CR2). This is consistent with lower C inputs from CCs in this study (CR1: 0.82-1.82 Mg ha^{-1} a^{-1}) compared

475   to reported mean C inputs from CCs of 1.87 Mg ha^{-1} a^{-1} in Poeplau and Don (2015). One likely reason for the lower C inputs

in Göttingen and Hohenheim is the relatively late sowing of cover crops (end of August to early September), which hampered

optimal biomass production.

However, the study's findings are subject to certain uncertainties because the models employed are pure soil C models. First,

plant growth was estimated from experimental data rather than dynamically simulated, which may limit the interpretation of

480   the results. Second, the representation of CC biomass was based on only two relatively dry years, potentially underestimating

the full variability in C inputs. Moreover, N availability, which may affect biomass growth and C utilization efficiency during

the conversion of crop residues to soil organic matter (Jian et al., 2020), is not considered in the current models.
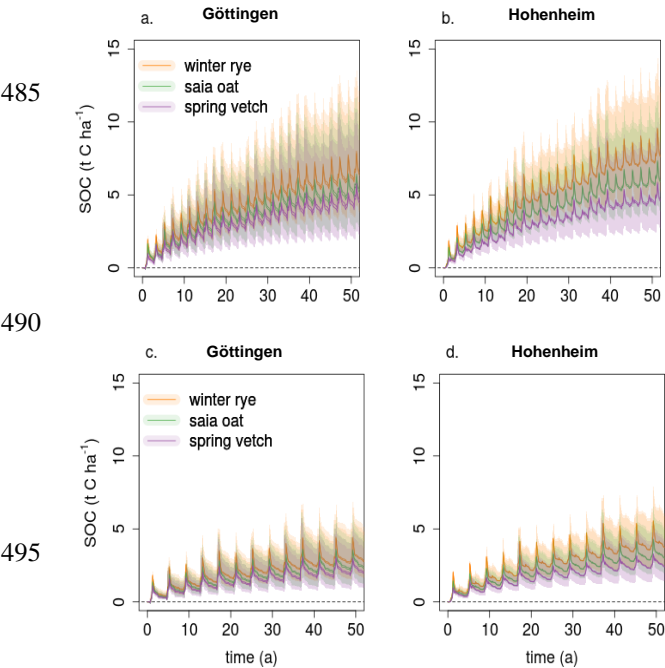
Figure 4. Modelled effect of cover crops (CCs) on the increase in SOC stocks (0-30 cm) compared to the control without CC for regionally common crop rotations (a, b) CR1 "CC/bare fallow – sugar beet – winter wheat – CC/bare fallow – silage maize with an application of 30

500   m^3 digestate from biogas plants before seeding of the maize" and (c, d) CR2 "CC/bare fallow – sugar beet - winter wheat – winter rape – winter wheat" with a CC in every 4th year at the Göttingen and Hohenheim experimental sites (2 fields per site). Shaded areas show the variability of the model ensemble.

Table 6. Simulated carbon sequestration rates caused by cover crops (CCs), averaged over a simulation period of 50 years with model structural uncertainties in brackets

Crop rotation	CC	Carbon sequestration rate by CCs [t C ha^{-1} a^{-1}]		Carbon sequestration rate by CCs [kg CO$_2$ ha^{-1} a^{-1}]	
		Göttingen	Hohenheim	Göttingen	Hohenheim
CR1	Winter rye	0.13 (0.07;0.22)	0.15 (0.1;0.24)	477 (257;807)	550 (367;733)
CR1	Saia oat	0.11 (0.06;0.2)	0.12 (0.08;0.2)	403 (220;733)	440 (293;733)
CR1	Spring vetch	0.09 (0.04;0.17)	0.09 (0.05;0.17)	330 (147;623)	330 (183;623)
CR2	Winter rye	0.06 (0.04;0.11)	0.08 (0.05;0.13)	220 (147;403)	293 (183;477)
CR2	Saia oat	0.06 (0.03;0.1)	0.07 (0.05;0.11)	220 (110;367)	257 (183;403)
CR2	Spring vetch	0.05 (0.02;0.09)	0.06 (0.03;0.1)	183 (73;330)	220 (110;367)

These considerations are crucial in selecting CCs, as they underscore the intricate relationship between N dynamics, residue decomposition, and microbial activity. This complexity highlights the need for a comprehensive understanding of CC selection and management to optimize N uptake efficiency while reducing N$_2$O emissions. Modeling approaches could serve as valuable tools in this context by predicting the most suitable CC types based on site-specific factors such as soil type, climate, and the subsequent main crop. Moreover, conducting incubation studies under controlled conditions using labelled N can further elucidate the primary drivers of N$_2$O emissions, thereby facilitating more informed, locally tailored CC decisions. Ultimately, achieving a balance between maximizing N capture during the cover cropping phase and minimizing N$_2$O emissions during residue incorporation is paramount. Additional research into the mechanisms behind elevated N$_2$O emissions from CC residues and the development of effective mitigation strategies is essential to advance more sustainable agricultural practices.

4 Conclusions

The current study highlights the complex role of CCs in agricultural systems, particularly in relation to soil N dynamics, N$_2$O emissions and C sequestration. While CCs, especially non-legumes like rye and oat, have demonstrated significant potential in reducing SMN levels and mitigating the risk of NO$_3^-$ leaching, their impact on N$_2$O emissions is multifaceted. Our findings highlight that frost-sensitive CCs can lead to increased N$_2$O emissions following frost events or, in all cases, the incorporation of crop residues for establishing the next cash crop combined with mineral N fertilization. However, the potential of CCs to mitigate indirect N$_2$O emissions and sequester C, suggests a beneficial aspect of their use in sustainable agriculture. This balance between N capture, N$_2$O emission and C sequestration, emphasizes the need for strategic management of CCs to harness their benefits fully while minimizing potential environmental drawbacks. Especially, the type of CC (frost tolerance, legume or non-legume and pest control aspects) needs to be chosen carefully depending on the following cash crops and climatic conditions. Future research should focus on developing crop rotation and site-specific management practices that optimize CC benefits for soil health, crop productivity, and climate change mitigation.

Data availability. Data are available here: https://doi.org/10.25625/HFEDA7

Supplement. The supplement related to this article is available online at:

Author contributions. VN conceived of the research, contributed to methodology development, performed data curation, performed formal calculations, data analysis and investigation, and drafted the original manuscript. MH provided critical input during the review and editing process, contributed resources and validation, and participated in drafting the manuscript. RD performed formal analysis, provided visualization support, and participated in drafting the manuscript. AM and PR contributed to the review and editing of the manuscript. H-JK provided supervision throughout the project, contributed to the review and editing process, and played a role in the design of the study. RR provided feedback, supervised the project at the Hohenheim site, contributed to the conceptualization, and acquired partial funding for the research, while LE performed data collection and curation at the Hohenheim site. KD provided feedback, supervised the project at the Göttingen site, contributed to the conceptualization, and acquired partial funding for the research. All authors reviewed and approved the final version of the manuscript.

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.

Acknowledgements. This study was conducted as part of the joint research project "Reduction of greenhouse gas emissions from crop production through site-specific optimized cover crop systems" (THG ZwiFru), funded by the German Federal Office for Agriculture and Food on behalf of the Federal Ministry of Food and Agriculture (Funding reference no. 281B200716). We extend our sincere appreciation to the local farmers in Göttingen and the crew at the Institute for sugar beet research in Göttingen for facilitating our experiments on their fields. Special thanks go to Thorsten Gronemann and Marlies Niebuhr for their assistance in the field, and to Dennis Grunwald for his efforts in data curation

Financial support. This project has been funded by the Federal Ministry of Food and Agriculture (BMEL), following a decision by the Parliament of the Federal Republic of Germany, and is administered through the Federal Office for Agriculture and Food (BLE) under the innovation support program (Funding reference no. 281B200716). This work was partially funded by the Deutsche Forschungsgemeinschaft (DFG, German Research Foundation) under Germany's Excellence Strategy – EXC 2070 – 390732324.

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