



Legacies of winter cover crops lead to opposing optimal N fertilisation rates and yields in first and second subsequent crops on contrasting soils

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Abstract Winter cover crops (CCs) provide substantial agronomic and environmental benefits, yet their influence on nitrogen (N) fertilization requirements and yield outcomes for subsequent crops remains underexplored. This study investigates the economic optimal nitrogen rates (EONRs) and corresponding yield effects for first (silage maize or sugar beet) and second (winter wheat) succeeding crops following CCs. Four CC species from different functional groups were compared to a bare fallow control on contrasting sandy and loamy soils across four German field sites over two consecutive cropping sequences. Results revealed opposing effects: reduced

EONR and increased N use efficiency on sandy soils in silage maize sequences, particularly following oil radish and rye CCs, but increased EONR on loamy soils for sugar beet sequences, with vetch CC showing the most favourable outcomes. Yield impacts varied by CC type and soil, with oil radish consistently enhancing yields across sites. However, CC effects on EONR were not correlated with pre-winter N uptake in CC biomass, challenging simple N budgeting practices. Environmental analysis highlighted potential greenhouse gas savings via reduced fertilizer inputs on sandy soils but increased upstream emissions on loamy sites. These findings emphasize the need for site-specific CC selection to balance economic and environmental benefits, with oil radish and vetch emerging as optimal choices in our trials for sandy and loamy soils, respectively.

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Introduction

Cover crops (CCs) are recognised for their numerous benefits, including the prevention of nutrient leaching losses (Nouri et al. 2022), soil erosion (De Baets et al. 2011; Jian et al. 2020a) and the enhancement of soil functions and biodiversity (Daryanto et al. 2018). Cover crops, also known as catch crops, significantly reduce nitrate leaching (Abdalla et al. 2019; Nouri et al. 2022) and therefore support nitrogen (N) transfer to subsequent crops. However, their effects on subsequent cash crop yields are inconsistent (Bourgeois et al. 2022; Van Eerd et al. 2023), and the precise extent of N fertilizer savings after winter CCs remains unclear. Nevertheless, legal frameworks like the German fertiliser ordinance (DüV 2017) implement reductions of the official N rate recommendations based on tabulated values for functional groups of CCs.

Many studies observed the effects of different CCs on subsequent crop yield, but mainly on a given fertiliser N level and sometimes in relation to an unfertilised control. Reported results are highly variable depending on pedo-climatic conditions, CC species, and subsequent cash crops (Marcillo and Miguez 2017; Wang et al. 2021; Chahal and Van Eerd 2023). The concept of economically optimal N rates (EONR) offers more potential for identifying adapted fertiliser N inputs to CC legacies.

EONR refers to the N application rate that maximizes the economic return from fertiliser inputs, balancing the cost of fertilizer against the yield benefits it provides (Neeteson and Wadman 1987; Dhakal and Lange 2021). This concept ensures maximum profitability while minimizing environmental impacts associated with excess N. Since EONRs are influenced by various factors, including pedo-climatic conditions and crop genetics (Morris et al. 2018). Species- and site-specific knowledge about the impact of CCs on EONRs of subsequently grown cash crops is necessary to sustainably adjust fertiliser N inputs in cropping sequences. The impact of CCs on subsequent cash crop performance strongly depends on CC composition (Ladan and Jacinthe 2017), as indicated by

their C:N ratio. This ratio is a common proxy for determining the N release potential during mineralisation (Dabney et al. 2010).

Besides often observed soil mineral N (SMN) and plant N uptake dynamics, additional information can be derived from less frequently performed N rate experiments in subsequent crops after CCs and from derived EONR instead of comparisons at a fix N fertilisation level. Such N rate experiments with more than three increased N levels are rare under humid temperate conditions. Trials with maize following different CCs in the US Midwest showed more often an increase of EONR after cover crops than a decrease (Bielenberg et al. 2023). Evaluations of N response in grain maize after rye CC revealed increased EONRs with lower yields compared to fallow on poorly drained soils (Pantoja et al. 2015). In other experiments conducted in the same region, this negative impact of a rye CC on N response in subsequent maize was found to be partially offset through split N applications (Quinn et al. 2023).

Resulting yield effects in the first succeeding crop after winter CCs are described variously throughout the literature in original studies as well as in meta-analyses (Kühling et al. 2023; Koch et al. 2024). Mostly those comparisons were done on identical N levels instead of identifying the resulting change in EONR from cover crops. This common study design with fixed N rates does not sufficiently reflect the potential interactions between altered optimal N input and resulting yield effects in cash crops following CCs. Furthermore, most studies only include the legacy effects of CCs on the first succeeding crop. Since mineralisation depending on residual C:N ratios and termination time of the CCs might occur after the main N uptake of the first succeeding crop we further included the second succeeding cash crop in our analysis.

The efficacy of the general principle of buffering residual N from preceding crops in CC biomass, thereby decreasing N leaching losses and increasing subsequent transfer through delayed re-mineralisation into the succeeding cash crops is, however, contingent upon pedo-climatic conditions and biomass composition (C:N ratio). Nevertheless, the site characteristics necessitate different performing CCs with respect to excess N leaching potential and gaseous N losses. Sandy, well drained soils prone to leaching are best managed with CCs for maximal

autumnal SMN reduction through high N uptake in CC biomass (Kühling et al. 2023). Selection on loamy soils with low N translocation potential is more in the direction of good N supply to the subsequent crop and minimal fertiliser N immobilisation (Koch et al. 2024). Moreover, potentially altered nitrous oxide (N₂O) emissions from CCs and subsequent crops are contradictorily described in the literature and strongly related to the pedo-climatic site characteristics as well (Basche et al. 2014; Han et al. 2017; Muhammad et al. 2019; Helfrich et al. 2024). Consequently, all paths of potential losses as well as compensation potentials must be considered in a holistic approach of CC integration in cropping systems/crop rotations.

Precise information about changes in optimal N fertiliser inputs is particularly important for identifying climate smart cropping systems due to their upstream emissions contributing to the greenhouse gas (GHG) balance. Specifically, savings of mineral N fertiliser can relieve cumulative GHG emissions by reduced burning of fossil fuels during Haber–Bosch ammonia synthesis. To gain a comprehensive understanding, it is essential to consider the findings on EONR in conjunction with the yield effects. Furthermore, commonly used N related indicators estimated at site-specific and CC species-specific EONRs enable a fair comparison of ecological effects. The objectives of this study were to (i) derive economic optimal N fertiliser rates (EONR) and corresponding yield effects in the first and second succeeding cash crop on contrasting site characteristics as influenced by different winter CCs compared to a bare fallow. Furthermore,

these effects were translated into (ii) N related environmental indicators and (iii) potential effects on upstream GHG emissions of external resources.

Materials and methods

Study sites

Four different field sites, similar in design, located in two typical cropping areas for maize and sugar beet in Germany were used in the current study (Table 1).

The weather conditions during the observed experimental periods in comparison to the long-term average conditions were warmer and drier in the first sequence and warmer and wetter in the second sequence (details in supplementary materials (Figure S1)).

Experimental design

Field trials with four unfertilised winter CCs from different functional groups (Table 2) and a bare fallow which served as control were established in two consecutive years (2018, 2019) at each site, leading to overall 8 site-years. To test the N conservation potential of the CCs, previous crops with a high nitrate leaching potential were chosen with winter oilseed rape (KI/UE) and field pea (GO/IH). No additional N was applied to the CCs in autumn. In the first subsequent crop (silage maize at KI/UE, sugar beet at GO/IH) four different N levels were applied after all five CCs. The four N levels of the second subsequent crop winter wheat were applied only within the N2

Table 1 Characteristics of the four study sites with long-term average (LTA) climate data (Agronomy Kiel 2023) and soil properties (according to IUSS Working Group WRB (2022))

	KI	UE	GO	IH
Location	Hohenschulen near city of Kiel	Westerweyhe near city of Uelzen	Hevensen/Niedernjesa near city of Göttingen	Ihinger Hof near city of Stuttgart
Lat, Long	54.32, 9.98	52.99, 10.50	51.64, 9.89	48.75, 8.92
1st succ. crop	Silage maize		Sugar beet	
2nd succ. crop	Winter wheat			
LTA temperature	9.4 °C	10.0 °C	8.4 °C	9.5 °C
LTA precipitation	769 mm	743 mm	738 mm	624 mm
Soil type	Luvisol	Cambisol/Planosol	Luvisol	Luvisol
Topsoil texture	Sandy loam	Sandy loam	Silt loam	Silt loam/silty clay loam

Table 2 Characteristics of the four tested cover crops from different functional groups

	Oil radish	Saia oat	Spring vetch	Winter rye
Botanical name	<i>Raphanus sativus</i>	<i>Avena strigosa</i>	<i>Vicia sativa</i>	<i>Secale cereale</i>
Cultivar name	Defender	Pratex	Mirabella	Traktor
Winter hardiness	No	No	No	Yes
Family	Brassicaceae	Poaceae	Leguminosae	Poaceae
Roots	Deep tap root	Shallow fibrous root	Medium fibrous root	Shallow fibrous root

levels of the previous crops, that were oriented on the optimal rate and established on four subplots (see Table S1 for details). The experimental design with overall 20 treatments in each subsequent crop followed a randomised block design with four field replications where N-treatments were nested within CC plots. Harvest-plot size was 3×7.5–14 m depending on the site.

Trial management

Details of the crop management at both experimental sites is given in supplementary Table S1. Sowing of CCs was done after emergence of weeds and volunteer pre-crops (oilseed rape at KI/UE, field pea at GO/IH) to kill those plants during seedbed preparation. A bare fallow control was integrated by chemically controlling weeds of previous crop and retaining stubble. This was effective at the KI, GO and IH site; however, at the UE site, significant growth of volunteer oilseed rape (OSR) occurred despite all herbicide applications and had to be removed mechanically in November/December. Therefore, observations at the UE site were excluded from some direct comparisons against the bare fallow treatment. The sole sown spring vetch CC was not competitive against volunteer OSR and hereafter referred to as OSR/spring vetch mixture at sites KI and UE. Cover crop termination was done chemically by applying glyphosate and about two weeks later, shallow mechanical residue incorporation with a cultivator (5–15 cm depth), except for winter rye where a mouldboard plough (25 cm depth) was used for incorporation of the living roots and high amount of above ground biomass instead. Nitrogen was applied as calcium ammonium nitrate (CAN, 27% N) in the given N levels according to Table S1. Total amounts were split up to two/three doses for spring/winter sown crops, respectively. All further crop management (e.g., pesticide applications)

was done uniformly across all treatments according to common practice at each site.

Field data collection

Soil mineral N (sum of nitrate + ammonia) was measured at three soil depths (0–30 cm, 30–60 cm, 60–90 cm) according to VDLUFA (2002) and considered as sum of all depths for spring SMN. Crop harvest took place with a plot combine harvester for winter wheat grain yield and manual sub samples were taken for harvest products of silage maize (hole plant biomass) and sugar beet (root biomass). All yield data was corrected by a plot factor of 0.9 to allow comparisons with farmers' fields and official recommendations/legal framework (Pahlmann et al. 2013). Post harvest analyses for dry matter content (gravimetrically) and concentrations of C, N (CN analyser), and white sugar concentrations (in sugar beets only) was uniformly done for all sites.

Calculation of economic optimal N rates (EONR)

For each main plot (CC×replication) regression models were fitted for yield, N uptake, and sugar concentration response on N supply. To cover the legacies of previous CCs, N supply was considered as sum of N fertiliser rate plus SMN in spring as predictor. Quadratic-plateau models (Eq. 1) were chosen for biomass yield of silage maize, root yield of sugar beet and grain yield of winter wheat.

$$Y_i(N_{supply}) = \begin{cases} a \cdot (N_{supply} - N_{max\ i})^2 + Y_{max\ i} & ; N_{supply} \leq N_{max\ i} \\ Y_{max\ i} & ; N_{supply} > N_{max\ i} \end{cases} \quad (1)$$

where N_{max} depicts the at least required N input N_{supply} to achieve highest yield Y_{max} . To cover the legacies of previous CCs, parameter a was estimated as common

for all four replications i , while N_{max} and Y_{max} were derived individually for each replication.

Quadratic models (Eq. 2) were fitted for response of white sugar concentration in sugar beets and N uptake in harvested products on N supply according to Pahlmann et al. (2016):

$$C_i^{sugar}, Uptake_i^N(N_{supply}) = a \cdot (N_{supply} - N_{max\ i})^2 + Y_{max\ i} \tag{2}$$

Again, a common parameter a for all replications i and individual estimations for N_{max} and Y_{max} was used.

The second order polynomials can be transformed into Eq. 3 for easy interpretation of the intercept (β_0), linear (β_1), and quadratic (β_2) terms:

$$Y_i(N_{supply}) = \underbrace{Y_{max\ i} + a \cdot N_{max\ i}^2}_{\beta_0} - \underbrace{2 \cdot a \cdot N_{max\ i}}_{\beta_1} \cdot N_{supply} + \underbrace{a}_{\beta_2} \cdot N_{supply}^2 \tag{3}$$

Economic optimal N supply ($EONR_{supply}$) was then derived after Eq. 4 as the N supply with maximum economic gross margins for each main plot (Neeteson and Wadman 1987; Dhakal and Lange 2021).

$$EONR_{supply\ i} = \frac{p - \beta_{1\ i}}{2 \cdot \beta_{2\ i}} \tag{4}$$

With p as the price ratio N/P of N fertiliser costs to harvest product price and the transformed coefficients from Eq. 3. Price assumptions are given in Table 3 and reflecting the market price situation at the end of the experiments as high. For comparison a long-term lower price scenario was additionally considered.

Table 3 Price assumptions for estimating the economic optimal nitrogen (N) rates. Dynamic price formation for sugar beets according to sugar content (SC) deviation from 16% as

Economic optimal N fertiliser rates $EONR_{fert}$ were ex post calculated from $EONR_{supply}$ minus SMN_{spring} before sowing (Eq. 5).

$$EONR_{fert\ i} = \max(0; \max(EONR_{supply\ i} - SMN_{spring\ i}; N_{max\ fert})) \tag{5}$$

Maximal economic optimal N fertiliser rates ($EONR_{fert}$) were restricted to the highest N fertiliser levels of the trials (Supplementary Table S1). In case of a negative computational optimal fertiliser rate, it was set to 0 (visual examples in supplementary materials).

All derived EONRs after the different CCs were compared to the site-specific official N rate recommendations for German agriculture as regulated in the

German Fertiliser Ordinance (DüV 2017). Permitted N rates are calculated after tabulated plant N demand for expected yields (five-year average) reduced by yearly measured spring SMN and species-specific tabulated pre-crop and CC effects. For all site-years this was conducted with main plot (=CC) specific SMN values based on the yearly observed yields in our trial.

Evaluation of N optimum effects by cover crops

To evaluate the effects on optimal N fertilizer rates and responding crop yields from CC in comparison to bare fallow a two-dimensional approach was chosen.

common for German sugar industry. DM: dry matter, P: harvest product, p: Price ratio N/P

	Unit	DM content in harvest product	Price levels			
			Low		High	
N fertiliser	€ kg ⁻¹ N	–	0.8	P	P	
Silage maize	€ Mg ⁻¹ DM	34%	80	0.029	150	0.039
Sugar beet	€ Mg ⁻¹ DM	23%	96 + (SC–16) • 9.6 + 21	0.029*	130 + (SC–16) • 13 + 26	0.055*
Winter wheat	€ Mg ⁻¹ DM	86%	209	0.004	372	0.006

*Sugar beet price ratios were dynamically adjusted according to the sugar content

Individual effect sizes as mean difference between CC and fallow for $EONR_{fert}$ and yield at $EONR_{fert}$ were derived for all CC treatments with bootstrap estimations following Ho et al. (2019). For visualisation the mean effect sizes with 95% confidence intervals as error bars were plotted with N-optimum effect on the x-axis and yield effect on the y-axis (Fig. 1). Confidence intervals can always be used to interpret significant differences (at $\alpha=0.05$) if they do not overlap (with other intervals or reference lines). To distinguish between economically beneficial or disadvantageous situations the plot matrix can be divided by a reference line through the origin with a slope according to the price ratio p between fertiliser (N) and product (P). In case of dynamic price formation according to the sugar content, a mean slope for sugar beet was used. All effect sizes above this reference line show a beneficial economic performance of succeeding crops following CCs (greenish shading), effect sizes below the reference line present an unfavourable economic performance of crops after CCs compared to bare fallow (reddish shading). For stable price relations between N fertiliser and harvest products the line is only marginally affected by price changes (proportional increase or decrease of both prices). If changes in fertiliser costs are larger

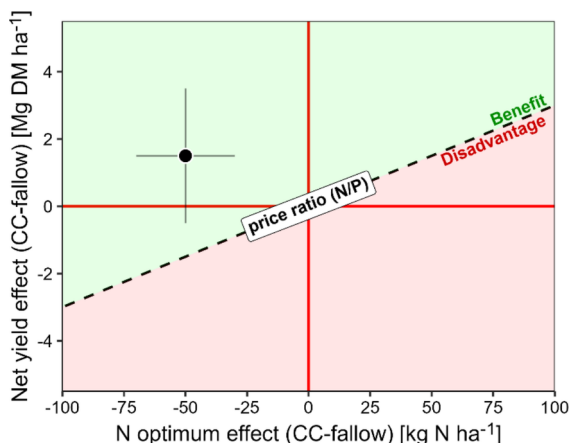


Fig. 1 Schematic illustration of simultaneous evaluation of CC impacts on optimal N fertiliser inputs and resulting crop yields with respect to bare fallow (red lines, no effect). Economic distinction according to the given price ratio between fertiliser costs (N) and product prices (P) into beneficial (greenish area) and unfavourable (reddish area) effects. Effect sizes (mean differences) as points with 95% confidence intervals as error bars in both directions

than for harvest products the line will rotate counter-clockwise for over proportional N price increases and vice-versa.

N related indicators

All subsequent indicators were calculated at $EONR_s$ for every main plot in each site-year. Nitrogen use efficiencies (NUE) were defined as quotient of the removal of N in harvested products ($N_{offtake}$) and N fertiliser input (Eq. 6)

$$NUE = \frac{N_{offtake^{fert}}}{N_{fert}} \quad (6)$$

The apparent fertiliser recovery efficiency (NRE) was calculated as the difference between removed N in harvested products from fertilised treatments and unfertilised conditions divided by the fertiliser N input (Eq. 7)

$$NRE = \frac{N_{offtake^{fert}} - N_{offtake^{NULL}}}{N_{fert}} \quad (7)$$

Nitrogen balances (NB) were calculated as N fertiliser inputs minus N offtake (Eq. 8)

$$NB = N_{fert} - N_{offtake_{fert}} \quad (8)$$

Calculation of upstream GHG emissions

To illustrate the potential contribution of affected $EONR_{fert}$ through CCs, fertiliser savings or additional needs were additionally assessed regarding their associated upstream GHG emissions during production processes. For this the current fertiliser mix as traded within the European Union was used with 3469 g CO_2eq per kg N (JRC 2019).

Results

CC effects on yield N response of subsequent crops

From overall 320 main plots, we were able to successfully fit 260 quadratic-plateau functions, the models for the remaining main plots did not converge.

Figure 2 shows mean functions over all replications and establishment years at the study sites for a general

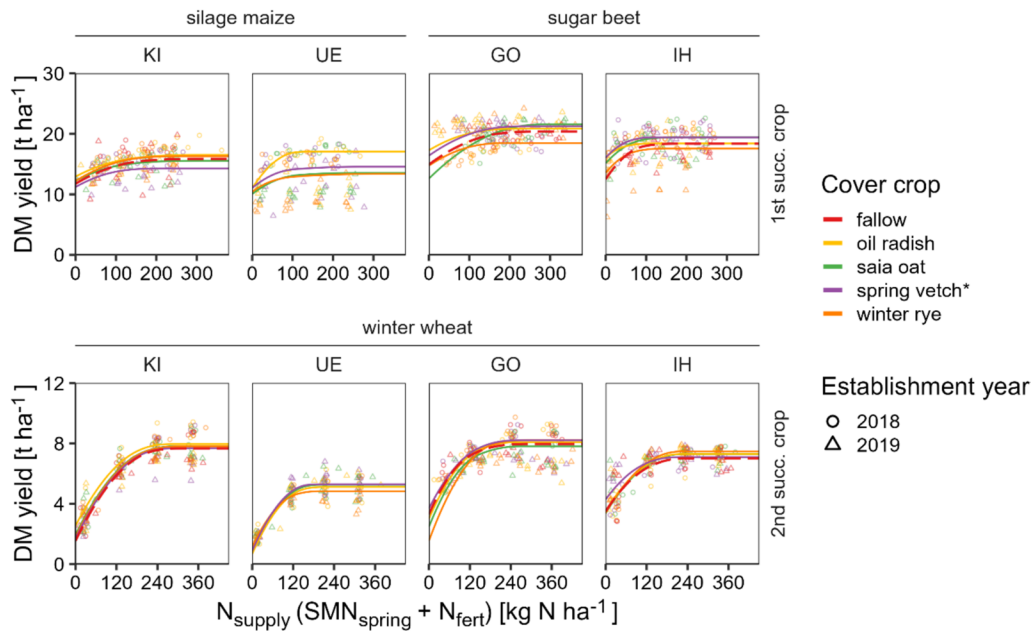


Fig. 2 Mean quadratic-plateau response functions for 1st and 2nd succeeding crops after different cover crops at all study sites. *spring vetch was a mixture with volunteer oilseed rape at sites KI and UE

illustration. Yield potential was highest at site GO with loamy soils and lowest at the sandy site UE. Functions for the 1st succeeding spring sown crops showed overall little yield response on N input but variation between the previous cultivated CCs (Fig. 2, top panels). The impact of the previously grown CCs and their different frost termination time and C:N ratios resulted in markedly different amounts of plant available N (sum of SMN and N fertiliser) in spring between the CCs (as fixed N fertiliser levels are hardly to see from the scattering dots). For winter wheat as 2nd succeeding crop the yield response on N input was more pronounced with only little variation between the CCs grown before the previous cultivated cash crops (Fig. 2, bottom panels). At the sandy silage maize sites only little legacies from CCs influenced the total N supply (N fertiliser levels clearly to identify). At the loamy sugar beet sites, the SMN in spring varied between the CCs, affecting their contribution to total N supply even in the second subsequent cash crop.

CC impacts on optimal N fertiliser inputs and resulting yields

Economic optimal N fertiliser rates of subsequent crops were differently affected by CCs (Table 4).

Spring sown crops of the first succeeding growing season always needed more mineral N fertiliser after winter-hardy rye CC to reach the economic optimum. For the second succeeding crop this switched at the sandy maize site with a slightly lower N need but remained on the loamy sugar beet sites. For all other investigated CCs, the $EONR_{fert}$ were lower on sandy soils in a maize-wheat cropping sequence with on average -14 kg N ha^{-1} for the 1st and -8 kg N ha^{-1} for the 2nd succeeding crop compared to cultivation after bare fallow. An opposite situation was observed in sugar beet sequences, where only 1st succeeding beets after non-winter-hardy vetch consistently resulted in slightly lower $EONR_{fert}$ (-13 kg N ha^{-1}) than after a bare fallow on both sites. At site IH the vetch effect occurred also for the 2nd succeeding winter wheat (-15 kg N ha^{-1}) and, further, a fertiliser saving effect for beets after oil radish was observed (-13 kg N ha^{-1}). For all other CC treatments, a higher fertiliser N input by $+23 \text{ kg N ha}^{-1}$ on average was needed to reach the economic optimum. In cases with low optimal $EONR_{fert}$ after fallow at site GO the relative differences after CCs led to high percentage change, but still reflecting moderate absolute values (Table 4).

Table 4 Mean economic optimal N fertiliser rate on fallow treatments (kg N ha⁻¹) and relative differences following cover crop treatments (%) for 1st and 2nd succeeding crops at the 4study sites for two contrasting price levels. #Since at site UE no fallow treatments were available (na) N fertiliser rates for CC treatments are reported in absolute values (kg N ha⁻¹)

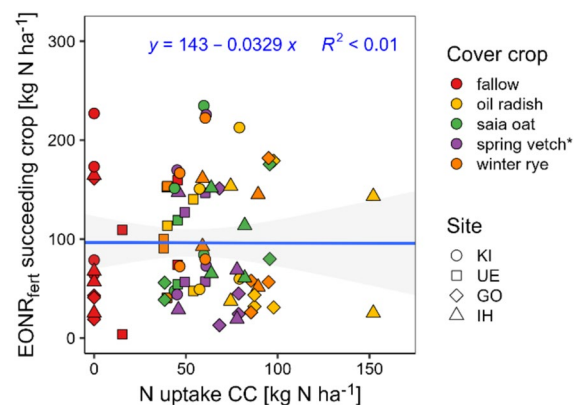
Price level	Low				High			
	Site	KI	UE [#]	GO	IH	KI	UE [#]	GO
1st succ. crop	Silage maize				Sugar beet			
Fallow	90.0	na	42.3	51.1	70.7	na	25.0	43.5
Oil radish	-21.2%	50.9	+24.3%	-25.9%	-21.7%	47.7	+26.7%	-27.9%
Saia oat	-9.7%	65.1	+103.6%	+42.5%	-6.7%	48.9	+156.0%	+48.0%
Spring vetch*	-22.9%	69.7	-16.0%	-42.9%	-24.1%	56.9	-14.0%	-44.7%
Winter rye	+4.8%	77.16	+78.1%	+61.2%	+7.6%	60.8	+128.0%	+72.8%
Price level	Low				High			
Site	KI	UE [#]	GO	IH	KI	UE [#]	GO	IH
2nd succ. crop	winter wheat							
Fallow	208.4	na	116.4	131.4	200.0	na	109.6	122.9
Oil radish	-6.7%	132.2	+21.5%	+18.8%	-7.0%	126.9	+22.1%	+20.0%
Saia oat	-3.4%	140.9	+6.5%	+9.4%	-3.5%	135.6	+6.6%	+10.1%
Spring vetch*	-1.1%	142.2	+18.9%	-11.0%	-1.2%	136.7	+18.5%	-12.0%
Winter rye	-2.6%	128.2	+18.2%	+23.0%	-2.7%	123.0	+18.5%	+24.5%

*Spring vetch was a mixture with volunteer oilseed rape at sites KI and UE

Derived EONRs showed no correlation with the maximal N uptake of CCs in the winter before (Fig. 3).

In contrast to the German legal requirements according to the fertiliser ordinance (FO) (DüV 2017) our estimated fertiliser rates markedly differed from the calculated recommendations (Fig. 4). For the 1st subsequent period of spring sown crops all EONR_{fert} values were below the official guidelines except sugar beets following saia oat at site GO. The mean differences for maize after CCs were -54/-47 kg N ha⁻¹ and for sugar beets -65/-77 kg N ha⁻¹ assuming low/high prices, respectively compared to FO recommendations. Within the 2nd succeeding winter wheat EONR_{fert} estimations and FO recommendations were a bit closer together, but still showing differences by -35/-42 kg N ha⁻¹ (low/high prices).

Resulting yields on the identified EONR showed different effects of CCs, with oil radish as the only species that increased all subsequent crop yields at all sites (Table 5). The yield effect of the first succeeding crop after legume spring vetch was only positive on

**Fig. 3** Correlation between nitrogen (N) uptake by cover crops (CC) and economic optimal N rates (EONR) of the first succeeding crop (silage maize at sites KI/UE and sugar beet at sites GO/IH) for high price scenario. *spring vetch was a mixture with volunteer oilseed rape at sites KI and UE

the loamy sugar beet sites, likely due to a poor CC canopy establishment on the sandy maize sites. Differences between the considered price levels are less pronounced than for EONR (Table 4).

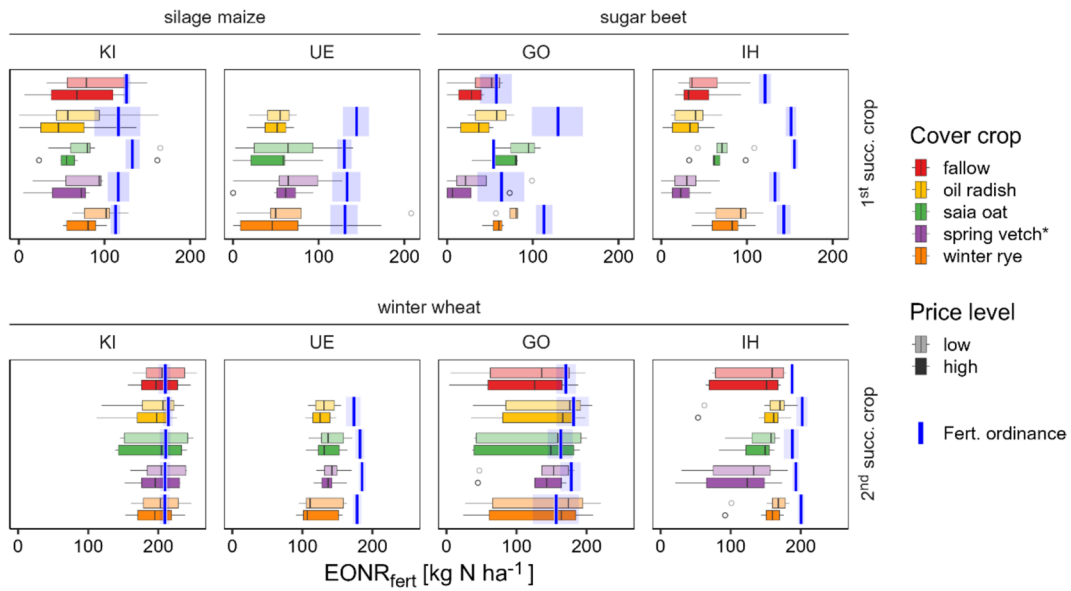


Fig. 4 Range of estimated economic optimal fertiliser N rates ($EONR_{fert}$) for the 1st and 2nd succeeding crop after different cover crops at the four study sites in contrast to official recommendations according to the German fertiliser ordinance

as blue lines (mean + standard error as light blue shading). Lighter/darker coloured bars indicate low/high price level for every cover crop. *spring vetch was a mixture with volunteer oilseed rape at sites KI and UE

Table 5 Mean dry matter yields (silage maize whole plant, sugar beet root, winter wheat grain) at economic optimal N fertiliser rates on fallow treatments ($Mg\ ha^{-1}$) and relative differences following cover crop treatments (%) for 1st and 2nd

succeeding crops at the 4 study sites for two contrasting price levels. #Since at site UE no fallow treatments were available (na) yields from CC treatments are reported in absolute values ($Mg\ ha^{-1}$)

Price level	Low				High					
	Site	KI	UE [#]	GO	IH	Site	KI	UE [#]	GO	IH
1st succ. crop	Silage maize				Sugar beet					
Fallow	15.6	na	20.2	18.3	15.3	na	20.0	18.2		
Oil radish	+4.5%	17.0	+1.8%	+0.2%	+4.9%	17.0	+1.1%	+0.3%		
Saia oat	-2.1%	13.2	+5.2%	+5.6%	-1.8%	13.0	+4.5%	+5.6%		
Spring vetch*	-9.8%	14.3	+4.0%	+5.7%	-9.7%	14.2	+3.9%	+5.8%		
Winter rye	+3.0%	13.2	-10.1%	-4.5%	+3.1%	13.0	-10.7%	-4.5%		
Price level	Low				High					
	Site	KI	UE [#]	GO	IH	Site	KI	UE [#]	GO	IH
2nd succ. crop	winter wheat									
Fallow	7.6	na	7.9	7.0	7.6	na	7.9	6.9		
Oil radish	+3.7%	5.1	+1.5%	+4.1%	+3.7%	5.1	+1.5%	+4.1%		
Saia oat	+2.0%	5.2	-1.9%	+4.1%	+2.0%	5.2	-2.0%	+4.2%		
Spring vetch*	+0.2%	5.3	+3.0%	+1.2%	+0.2%	5.2	+2.9%	+1.2%		
Winter rye	+1.8%	4.8	+3.3%	+6.6%	+1.8%	4.8	+3.3%	+6.7%		

*Spring vetch was a mixture with volunteer oilseed rape at sites KI and UE

Combined N input and crop yield effects of CCs

The economic success of CC effects on optimal N rates and resulting yields depends on the price proportion with respect to the price relation. Dividing the effects by the bare fallow treatment as reference into four quadrants (Fig. 1) there are clear benefits with higher yields from lower N inputs (top left, full greenish shading) or clear disadvantages with lower yields from higher N inputs (bottom right, full reddish shading). The remaining two quadrants (top right and bottom left) can be divided into beneficial/disadvantageous by the price ratio, meaning that for example also higher N inputs after CCs can lead to higher revenues with disproportionate higher yields.

Maize on sandy soils was most successful after oil radish and winter rye CC, the second succeeding winter wheat benefitted from all CCs (Fig. 5 left panel). However, none of the treatments was significant. Sugar beets on loamy soils yielded more with less N fertiliser input after oil radish and spring vetch CC but needed significant more N to reach the economic optimum following saia oat and winter rye

(Fig. 5 right panels). For the latter one, higher N needs could not be compensated by yield increases. The second succeeding winter wheat showed non-significant higher N needs with above average higher yield response for economic success.

Effects of CCs on further N related indicators

The effects of CCs in cropping sequences resulted in opposite effects on further N related indicators between the two soil properties: Mostly positive effects including increased NUE or reduced N balances for all CCs occurred in maize-wheat sequences on sandy soils but only after the legume CC spring vetch in sugar beet-wheat sequences on loamy soils (Fig. 6). Differences of NRE between subsequent crops after CCs compared to fallow were very small. Negative relative NRE values indicate larger differences in unfertilised comparisons than with EONR and underline the effectiveness of the CCs (Fig. 6B).

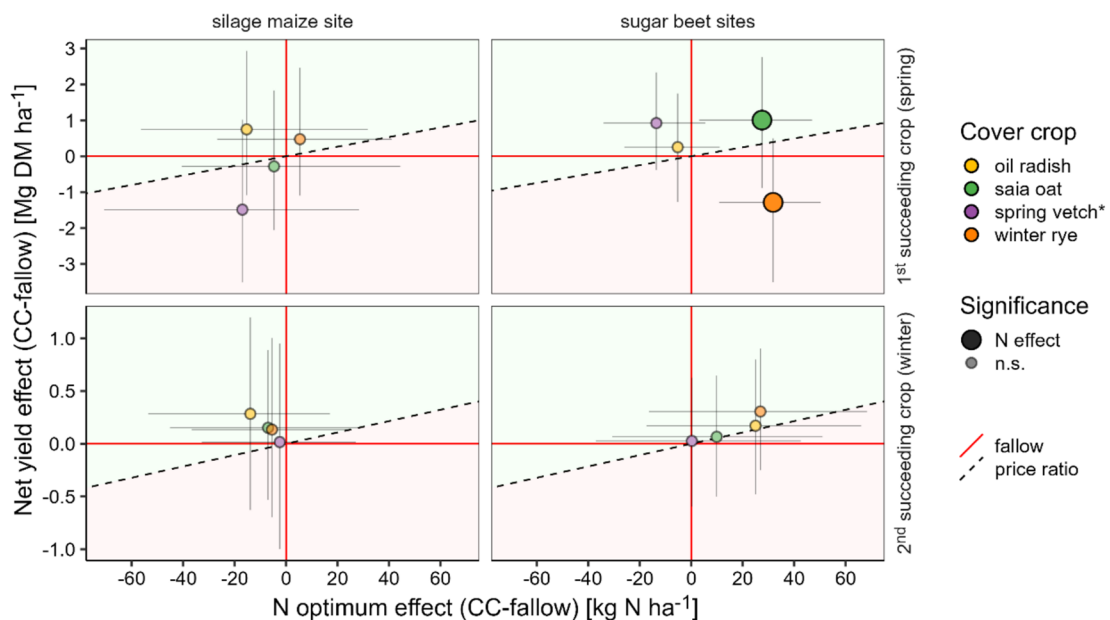


Fig. 5 Effect sizes (mean differences) of cover crops (CC) compared to fallow for combined evaluation of economic optimal N fertiliser rates (N optimum effect) and corresponding crop yields at high price levels. Fallow treatment as red reference lines, price ratios of N costs to product prices as dashed

reference line to distinguish between beneficial (greenish shading) and unfavourable (reddish shading) combinations; 95% confidence intervals as error bars. *spring vetch was a mixture with volunteer oilseed rape at the silage maize site



Fig. 6 Median N-related indicators (A: nitrogen fertiliser use efficiency (NUE), B: apparent nitrogen fertiliser recovery efficiency (NRE), C: nitrogen balance (NB) of the cropping sequences (spring crop maize or sugar beet followed by winter

wheat) after different cover crops as difference to fallow. Error bars indicating the 25th to 75th percentiles range. *spring vetch was a mixture with volunteer oilseed rape at the silage maize site

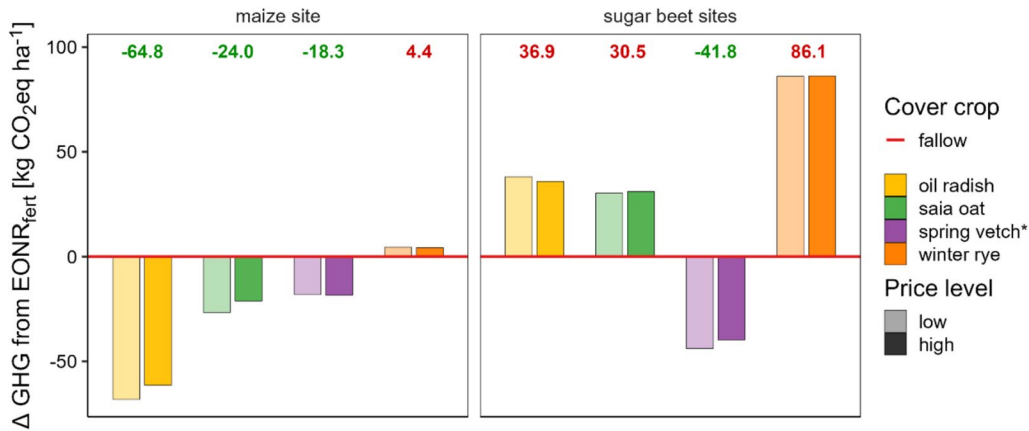


Fig. 7 Potential greenhouse gas (GHG) savings from upstream emissions during nitrogen fertiliser production for mean cropping sequences (spring sown maize or sugar beet followed by winter wheat) after different cover crops as difference to fallow.

low. Green/red numbers show mean values across both price levels. *spring vetch was a mixture with volunteer oilseed rape at the silage maize site

Climate impact through altered upstream emissions

Because of different mineral N fertiliser inputs into cropping sequences with CCs in contrast to bare fallow also the amount of upstream GHG emissions from energy intensive fertiliser production changes. Figure 7 shows the positive contribution of lowering climate impacts on sandy maize sites and potentially negative climate impacts from additional mineral N inputs after non-legume CCs on loamy sugar beet sites. However, in this analysis only the change in economically optimal synthetic N fertilisation has been included.

Discussion

N response influenced by site characteristics

Contrary to most other studies, we fitted individual N response regression models for every replication of the CC treatments for each site-year to use the block variation for further statistical analyses instead of interpreting mean response curves or EONR. However, since we observed typical but different 1st succeeding crops after CCs on the two soil categories, we cannot completely disentangle impact of site properties from crop characteristics.

The opposite effect of N fertiliser reduction after legume CC (vetch) and increase after winter-hardy

CC (rye) as observed for the loamy sugar beet sites in this study (Fig. 5) was also summarised from eight individual studies by Dabney et al. (2010). The resulting yield effects in the same direction of outperforming legumes compared to non-leguminous CCs were reported in the meta-analysis by Daryanto et al. (2018) and further original studies (Coombs et al. 2017; Wittwer and van der Heijden 2020; Jian et al. 2020b) using large datasets. Legume CCs' benefits typically combine biological N₂ fixation and rapid residue mineralisation with small C:N ratios. Selected CCs from different functional groups (Table 2) were also reported to have no or negative impacts on subsequent crop yields (Abdalla et al. 2019) and response to N fertiliser rates (Allison et al. 1998; Gieske et al. 2016; Snapp and Surapur 2018).

Besides those general effects of CCs on subsequent yields as described in the literature, our study provides additional details about the specific yield response to continuously increased fertiliser N input from the response function for each CC species (Fig. 2). While on sandy maize sites the response curves after CCs and fallow were on similar level, advantages after CCs resulted from lower EONR with same yields. However, on loamy sugar beet sites, advantages after CCs resulted mainly from response functions on a higher level with higher EONR leading to disproportionately higher yields. Specifically on the loamy sugar beet sites a clear differentiation between unfavourable winter-hardy rye CC and the most beneficial frost-killed legume vetch CC became evident. The impact of CCs residual composition (C:N ratio rye > vetch, see Figure S4) is more pronounced on soils with higher clay content. This could explain a higher fertiliser N immobilisation potential leading to a higher EONR after rye CC. However, depending on the price ratio, this may be economically advantageous. Quinn et al. (2023) described similar effects of N response functions in grain maize on a lower level after rye CC. The opposite effects between our sandy and loamy characterised study sites were also mentioned by Pantoja et al. (2015) with little improvements from CCs in finer textured soils in contrast to at least slightly decreased optimal N rates on sandy soils. Differences in mineralisation dynamics in interaction with plant N uptake according to the different site characteristics are described in detail in (Koch et al. 2022, 2024).

N response of different subsequent crops

The difference between sowing dates of earlier sugar beet and later silage maize are likely to cause differences in synchrony of N supply from mineralisation and plant N demand. As the combination of soil temperature and soil moisture shows clear temporal dynamics, root growth is also likely to be affected, apart from species-specific differences. In terms of net N mineralisation, the behaviour of the two observed crops as first succeeding crops after CCs was opposite. During maize growth at sites KI and UE periods of negative net N mineralisation during stem elongation until anthesis were observed (Kühling et al. 2023). Sugar beet grown after CCs showed higher N uptake than after bare fallow during early growth (Mar–Jul) and lower N uptake after CCs than after fallow later in the vegetation period (Aug–Oct) (Koch et al. 2022). The longer N uptake of maize during the later vegetation season takes place under higher mean soil temperatures. This is related to more favourable conditions for soil microbial activity and contributes to the better CC legacy utilisation in maize compared to sugar beet. During the mineralisation of CC residues, the soil microbial biomass consumes plant available N, which can lead to temporary fertiliser N immobilisation specifically for residues with wider C:N ratios. For the maize cropping season immobilisation rates up to 78% were observed (Kühling et al. 2023). For sugar beet temporary immobilisation rates could be even higher. If the CC residual is not utilised by the first succeeding crop. This led to the assumption that the remaining positive legacy should take effect in the second succeeding winter wheat. However, this was observed only partly in our field trials. After silage maize on sandy soils the EONRs in winter wheat were slightly lower with only minimally higher yield (Fig. 5 bottom left). In winter wheat after sugar beet the EONRs were still higher, indicating less mineralisation than after fallow, but the resulting higher yield shifted the productivity on a higher level as well (Figs. 2 and 5 bottom right).

EONRs lower than official recommendations

With respect to the FO as legal framework for N fertiliser application in Germany (DüV 2017), our estimated EONRs were much lower for the 1st succeeding crops silage maize and sugar beet and slightly

lower for the 2nd succeeding crop winter wheat (Fig. 4). The huge overestimation of N fertiliser need by official European recommendations for silage maize was also found by (Bukowiecki et al. 2025a, b). Conversely, a comprehensive analysis of more than 400 N rate experiments with winter wheat but without considering pre-crop or CC effects showed higher EONRs compared to the FO recommendations (Kage et al. 2022). The large difference between winter and spring sown crops is mainly due to the difficulty of quantifying N mineralisation during summer, which is most relevant for silage maize (Bukowiecki et al. 2025a).

Even though we found clear differences of CC legacies on following crops, the contrasting effects depend on different site characteristics make a simplified implementation in legal frameworks difficult. A popular approach to account for the N fertiliser saving potential of CC based on their above-ground biomass or above-ground N uptake due to its practicability showed no correlation from our dataset ($R^2 < 0.01$, Fig. 3). Hence it is necessary to consider species-specific CC effects for subsequent N fertiliser level recommendations. The category in the current FO of “non-legumes frost killed” with 0 kg N is too unspecific for crops like oil radish (5–68 kg N ha⁻¹) as well as saia oat (–17 to 15 kg N ha⁻¹). Furthermore, the assumption for “frost-killed legumes” with 10 kg N ha⁻¹ credit seems too low with spring vetch in our study resulting in 13–35 kg N ha⁻¹. Only the category of “winter-hardy non-legumes, spring incorporated” with 20 kg N ha⁻¹ matched with our findings for rye (26 kg N ha⁻¹). Therefore, our results from selected CC species indicate the necessity for a more precise categorisation to better reflect CC residue quality (e.g. C:N ratio, Kühling et al. 2023). In combination with pre-winter N uptake in CC biomass this would better cover the N saving potential to reach the economic optimum. However, findings from other CC species and mixtures and more pedo-climatic conditions must be included for a general estimation approach.

N use efficiency and balance

Increased NUE following CCs was often described in the literature, particularly from systems with no or low N input (Sieling 2019). In contrast, we evaluated the impact of CCs on NUE and NRE for

comparatively high N inputs at the economic optimum (Fig. 6). In our field trials we observed opposite effects on sandy maize sites compared to loamy sugar beet sites. As processes like fertiliser N immobilisation led to higher EONRs for sugar beet after non-legume CCs, resulting NUEs were lower compared to sugar beet after fallow. In terms of NRE the positive yield response overcompensated the higher mineral N inputs for sugar beets following oil radish and saia oat. It was not possible to fully disentangle the effects of subsequent crop and soil from the given experimental design. Whereas the observed positive effects of legume vetch CC in sugar beet sequences on loamy soils are in line with previous studies (Kramberger et al. 2009; Langelier et al. 2021), the non-legumes oil radish and saia oat outperformed within maize sequences on sandy soils. The legume inferiority from our trials might be partly explained due to the poor stand establishment of spring vetch on the sandy maize sites, resulting in a mixture with volunteer oilseed rape. It is also worth noting that a sole legume CC on sandy soils prone to nitrate leaching is not a viable option in any case (Luis et al. 2013; Thapa et al. 2018). Legume CCs in mixtures with non-legume species (e.g. rye or radish) have been shown to reduce nitrate leaching (Elhakeem et al. 2023; Engedal et al. 2023) and can support challenging canopy establishments. Overall, the vetch has to be considered as an exceptional CC, especially when it comes to holistic assessments, as the additional N input into the system is likely to increase negative GHG emissions. Furthermore, the N related indicators as averaged over a cropping sequence of two crops with 50% contribution by a spring sown one are in general ecologically inconspicuous, due to the relieving function of summer crops. Therefore, we only evaluated the net effect of CCs in contrast to the bare fallow treatment (absolute values in supplementary Table S2).

Economic performance vs. environmental impacts

Economically, the costs for establishing CCs have to be covered either by reducing production costs, increasing main crop yields or subsidies linked the CC's positive environmental effects (Daryanto et al. 2018). Here, we primarily evaluated the economic performance of different CCs in contrast to bare fallow in terms of implemented N fertiliser costs. This is

only one aspect and for a complete break-even analysis of cover cropping also costs of CC establishment and termination as well as all further machinery and operating costs must be considered. Additional costs for CC establishment and termination in our experiments were calculated from official numbers and ranged between 154 and 353 € ha⁻¹, with lowest costs for oil radish and highest costs for saia oat (Supplementary Figure S3). On average, establishment costs accounted for about 75% of the total expenses. In contrast, only after oil radish was the increase in N free revenues high enough to cover these costs. Therefore, cover cropping is mostly practiced within agri-environmental schemes or to fulfil European subsidy requirements at lowest economic effort instead of aiming at site-specific best practice species selection. Nevertheless, external (societal) costs associated with environmental impacts, such as GHG emissions or nitrate leaching, are not incorporated in the evaluation by default.

Upstream emissions from fertiliser production as presented in this study are only one aspect to be included in GHG balances (Fig. 7). In a holistic greenhouse gas balance, e.g. the vetch would be burdened with higher emissions via the additional N input by means of symbiotic N₂ fixation. Furthermore, it is even more important to account for direct and indirect nitrous oxide (N₂O) field emissions as well as the long-term carbon sequestration potential. Again, opposite effects of direct N₂O emissions as well as indirect emissions resulting from nitrate leaching were observed on the sandy maize sites and loamy sugar beet sites. On sandy sites KI and UE cumulative direct N₂O emissions from CCs were only slightly higher than from bare fallow (Helfrich et al. 2024), but SMN and therefore leaching potential including indirect N₂O emissions was significantly reduced (Kühling et al. 2023). The opposite trend was observed on loamy sites GO and IH where direct N₂O emissions were markedly higher and the overall leaching potential for fallow and CCs was low (Koch et al. 2022; Nasser et al. 2024). In combination with the GHG compensation potential of carbon sequestration through regularly long-term cover cropping this resulted in a net relieving climate effect on sandy maize sites but to a net burdening climate effect on loamy sugar beet sites. Of course, SOC accumulation follows a saturation function and reaches approximately after 50–100 years a new steady state.

In summary, the most optimal economic and ecological performance could be achieved through the cultivation of oil radish CC on sandy maize sites through effective N transfer instead of leaching losses and vetch CC on loamy sugar beet sites due to additional N input and timely release from residue mineralisation.

Conclusion

Combined consideration of N optimum and corresponding yield effect enables for identification of economic optimal N allocation in cropping sequences with and without CCs. Unlike in most studies, we considered the first and second subsequent crop to better cover the entire CC legacies. While the N saving effect after CCs was not always evident, the shift in productivity resulted mostly in higher yields which could even offset higher N needs. However, practice-oriented approaches such as approximately reducing N fertiliser rates according to the N uptake by CC biomass before winter should be avoided since we could not identify any correlation between above-ground N uptake of CCs and economic optimal N fertiliser rates for subsequent crops from our trials. To derive a general crediting of CC effects on fertiliser N recommendation, further results from varying site conditions and CC species as well as species mixtures are necessary. Based on our results, a site-specific CC species selection tailored to different site characteristics such as soil texture and leaching potential would lead to most suitable oil radish before maize on sandy soils and spring vetch before sugar beet on loamy soils.

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Author’s contribution IK: Methodology, Validation, Formal analysis, Visualization, Data Curation, Writing—original draft, Writing—review & editing IP: Formal analysis, Conceptualization TR: Investigation, Data Curation MH: Investigation, Writing—review & editing HF: Writing—review & editing, Funding Acquisition MS: Resources, Funding Acquisition H-JK: Investigation, Writing—review & editing, Funding Acquisition

LE: Investigation RR: Funding Acquisition MR-K: Investigation, Writing—review & editing AH: Funding Acquisition HK: Conceptualization, Supervision, Writing—review & editing, Funding acquisition, Project administration.

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Data availability No datasets were generated or analysed during the current study.

Declarations

Conflict of interest The authors declare no competing interests.

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