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A global synthesis of genotypic variation in crop greenhouse gas emissions under variable nitrogen fertilisation

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Targeted crop selection offers a promising potential pathway to reduce greenhouse gas (GHG) emissions from global croplands. Yet, the influence of crop genotypes on GHG emissions remains poorly studied, limiting our ability to understand its global potential. To address this challenge, we conducted a global synthesis of GHG and crop yield data from 42 field experiments across 180 genotypes of major cereal (predominantly rice) and oilseed crops (soybeans and canola) and nitrogen (N) fertilisation rates (40kg ha⁻¹ to 390kg ha⁻¹) (n = 390). To test the influence of genotype, we removed measurements from genotypes with fewer than three independent replicates (n = 97) and apply linear mixed-effects models to control for study and latitude effects. Across a range of environmental and experimental conditions, we analysed the influence of N application rate on crop nitrous oxide (N₂O) and methane (CH₄) emissions, alongside yield. We found significant differences in N₂O-N cumulative fluxes between crop types and mean annual precipitation ranges. When expressed per unit of crop yield, N₂O-N and CH₄-C cumulative fluxes revealed a significant difference between N application rate groups (a = < 50, b = 50-100, c = 100-150, d = 150-200, e = 200-250, f = 250-300, g = > 300), with a positive yield response to N fertilisation. While yield-scaled N₂O-N cumulative fluxes declined with N application rate, yield-scaled CH₄-C cumulative fluxes increased; however, all CH₄ measurements were derived from rice systems. Regression relationships between cumulative N₂O, CH₄, crop yield and N application rate were consistent with previous global syntheses, showing that N₂O and CH₄ emissions increased exponentially with N application, while crop yield

exhibited a quadratic response. Our results indicate that N application rate was the primary driver of N₂O emissions and crop yield, while genotypic differences significantly influenced CH₄ emissions. These findings underscore the importance of integrating genotype selection with nitrogen management to improve GHG mitigation while optimising crop productivity.

KEYWORDS

nitrous oxide, methane, climate change mitigation, nitrogen fertilisation, greenhouse gas emissions, genotypic variation

Introduction

Agricultural intensification to meet global food demand has made farming one of the largest contributors to anthropogenic greenhouse gas (GHG) emissions (Lynch et al., 2021; Tilman et al., 2011), contributing approximately 58% of global non-carbon dioxide (CO₂) GHG emissions. GHGs such as nitrous oxide (N₂O) and methane (CH₄) further have global warming potentials 273 and 81 times greater than CO₂, respectively over a 20-year time period (Beach et al., 2008; IPCC, 2023). Agricultural GHG emissions exacerbate climate-related environmental problems, including biodiversity loss, eutrophication and reductions in soil carbon stocks (Johnson et al., 2014; Vitousek et al., 1997). Several cost-effective and sustainable agricultural mitigation opportunities and practices are accessible for agriculture compared to other sectors (Lai et al., 2022; Smith, 2012; Vergé et al., 2007; Zutshi and Creed, 2015).

Nitrogen (N) fertilisation remains a cornerstone of yield maximisation in modern cropping systems but is also a major source of N₂O emissions (Guo et al., 2022; Sun and Huang, 2012). Projections suggest that N fertiliser use could triple by 2050 (Khampuang et al., 2021) and so there is an urgent need to improve Nitrogen Use Efficiency (NUE) in crops to mitigate the negative effects of N application (Zhang et al., 2015). Previous meta-analyses have identified optimal N application rates for key global crops such as wheat, rice, and maize in the range of 130 to 200 kg N ha⁻¹, emphasising not only rate optimisation but also soil, climate, and genotype selections as complementary mitigation strategies (Guo et al., 2022). A promising strategy for reducing agricultural GHG emissions is the selective breeding for crop genotypes that exhibit higher NUE, enabling lower fertiliser inputs while maintaining high yield (Shcherbak et al., 2014; Swarbreck et al., 2019). Empirical studies have shown that crop genotypes can significantly vary in their N₂O and CH₄ emissions due to physiological and morphological characteristics such as transpiration rate, xylem vessel diameter, and root architecture (Borah and Baruah, 2016; Chen et al., 2021). Modern wheat genotypes have demonstrated lower N₂O emissions, potentially

due to physiologically more efficient N uptake rather than observable shifts in plant morphology (Chen et al., 2021). Other traits such as flag-leaf senescence and nitrogen accumulation at anthesis have also been linked to NUE (Gaju et al., 2011).

Optimal N fertilisation management can play an important role in NUE for oilseed rape genotypes (Berry et al., 2010). Whilst a large portion of these studies show a significant difference in N₂O and CH₄ emissions between genotypes, the resulting data and conclusions are frequently limited due to a limited number of genotypes used or low levels of replication (Chen et al., 2021; Gogoi and Baruah, 2012). Many studies which observe GHG emissions between different crop varieties investigate other factors which may be affected by the crop variety such as water management, further complicating direct comparisons (Ma et al., 2012; Phungern et al., 2023; Vo et al., 2024).

Genotypic variation can influence soil nitrification and denitrification by actively changing soil properties, such as N availability (through N uptake) and pH change via root exudation, respiration and NUE capacity (Philippot et al., 2013). Different genotypes can also be more or less effective at transporting N₂O from the soil via root uptake and releasing into the atmosphere (Baruah et al., 2010; Verma et al., 2006). The varieties with a n optimal root architecture will have greater NUE and have a reduced quantity of N₂O byproduct. Plants can also produce N₂O directly via N assimilation (Smart and Bloom, 2001), and different genotypes can have variable N₂O production during nitrogen assimilation (Oszvald et al., 2022). Genotypic variation can also influence plant-mediated transfer of CH₄ from the soil to the atmosphere due to differences in aerenchyma, root exudates and root oxygen (Aulakh et al., 2000; Girkin et al., 2018, 2020). Optimisation of agricultural management practices through selective breeding for crop genotypes with optimised NUE, sustained crop yields and low GHG emissions would assist in achieving a more sustainable agricultural produce (Ceccarelli and Grando, 2020).

Various studies have reported genotypic variation in crop GHG emissions, but their findings are limited by narrow genotypic comparisons and inconsistent experimental replications, often

focusing on a small number of genotypes within a single environment (Gogoi and Baruah, 2012; Chen et al., 2021; Phungern et al., 2023). To uncover the role of genotypic variation in GHG emissions from crops, especially under variable N fertilisation, a broader data synthesis is needed. While the concept that genotype impacts on GHG emissions are context-dependent and most pronounced at intermediate or suboptimal N rates is established in the literature. Here we provide the first global synthesis quantifying the magnitude and consistency of the genotypic effect on GHG emissions across studies.

Methods

Literature search and data collection

We conducted a systematic literature review using the Scopus database following PRISMA guidelines (Haddaway et al., 2022). We searched for peer-reviewed journal articles published up to April 2024 using the following keywords: (wheat OR rice OR barley OR oat OR linseed OR “oil seed rape” OR maize OR corn) AND (genotype OR genotype OR variety OR varieties) AND (“nitrous oxide” OR N₂O) AND NOT (livestock OR cattle). These crops were selected due to their high importance for global food systems and crop rotation systems. From 221 initially identified records, 42 studies met the inclusion criteria (Supplementary Figure 1), reporting GHG emissions from at least two genotypes of the same crop species under field conditions and provided sufficient data to quantify cumulative N₂O or CH₄ fluxes. See Supplementary Table 2 for a summary of the 42 studies included.

Many studies primary focus was not genotypic variation in greenhouse gas emissions and instead their primary focus was on specific management interventions. These interventions were not considered due to insufficient information across studies. A significant proportion of our compiled dataset came from studies focused on rice systems (35 of 42 studies) and there was a limited number of studies that included more than one crop (Supplementary Table 2). Most sources also studied a limited number of genotypes (< 3). This data sparsity limited our genotype analysis as many genotypes across several studies would be optimal for robust analyses. Many studies were conducted over multiple years however, providing replication of genotypes within studies.

Data extraction and standardisation

From each of the 42 studies identified, we extracted relevant metadata and experimental data including: crop species, genotype names, N fertiliser application rates, mean annual precipitation (MAP, mm), mean annual temperature (MAT, °C), measurement techniques, cumulative and daily GHG fluxes (N₂O-N, CH₄-C, and CO₂ where available), study duration, and crop yield (where reported). Data were extracted directly from tables, text, figures (via WebPlotDigitizer), or Supplementary Materials. Where necessary, units were standardised to kg ha⁻¹ for cumulative emissions. Cumulative N₂O-N fluxes were derived by converting N₂O mass to nitrogen mass using a factor of 14/44.01, and CH₄-C fluxes were converted using 12/16 from CH₄ mass to carbon mass (IPCC, 2023). For cases where only cumulative N₂O-N or CH₄-C

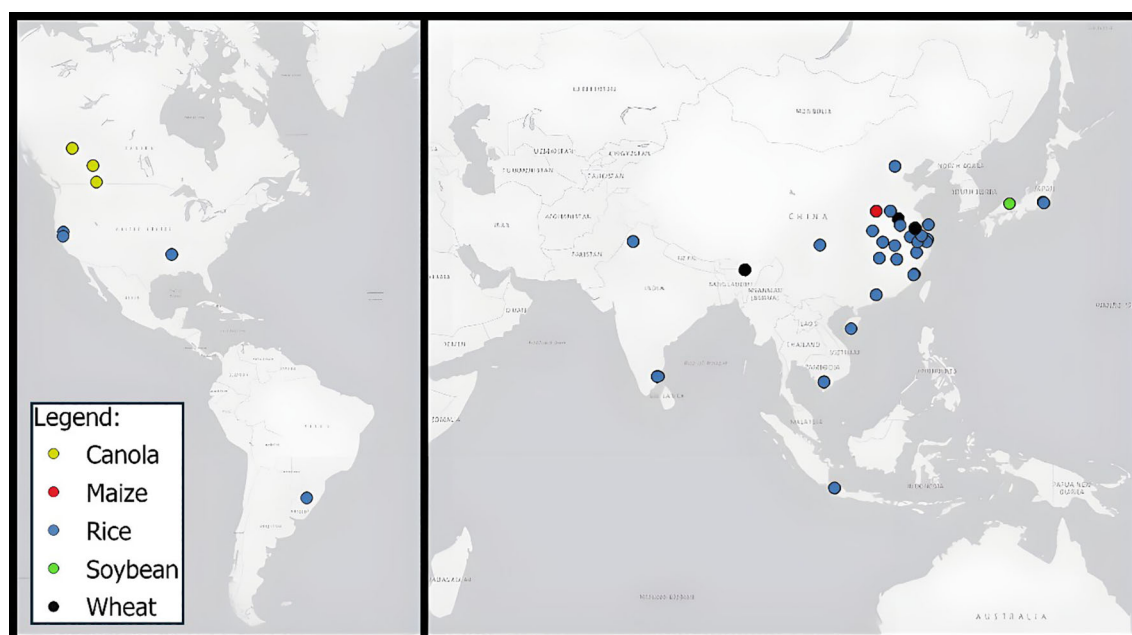


FIGURE 1
Distribution of studies reporting crop genotypic variation effects on GHG emissions, compiled in this study, showing a bias towards Asia and rice (crop type indicated by symbol colour).

were reported, average daily fluxes were back-calculated based on the reported measurement period. The compiled dataset included 391 data entries across 180 unique genotypes. Most data entries were for rice (n=319), followed by wheat (n=27), maize (n=20), canola (n=18) and soybean (n=3). Geographically, most data entries were from studies conducted in China (n=171), followed by Vietnam (n=80), India (n=75), Canada (n=18), Indonesia (n=16), USA (n=12), Japan (n=11) and Brazil (n=4) (Figure 1). Four data entries were removed as obvious outliers as they were associated with atypical treatments (e.g. chemical nitrate transport inhibitors) that distorted emission outcomes (Iqbal et al., 2023).

Study locations were restricted, with 23 from China, 9 from India, 3 from the USA, 3 from Japan and 1 from Vietnam, Brazil, Canada and Indonesia (Figure 1). This sampling bias reflects the high proportion of studies focusing on rice systems, as 90% of global rice production is conducted within Asian countries, which make up the majority of the results in our study (Fukagawa and Ziska, 2019). The majority of studies in our dataset used static chambers for GHG measurements (n=41) and few studies employed automated systems (n=1). Static chambers may underestimate episodic fluxes due to limited temporal coverage.

Data analysis

All analyses were performed in R 4.2.2 (R Core Team, 2024). Descriptive statistics and one-way ANOVAs were used to compare N₂O-N cumulative and CH₄-C cumulative fluxes across crop type, measurement method, chamber type, and N fertilisation, MAT and

MAP groups categorised using terciles to assess potential climatic and management effects. One-way ANOVA's and Tukey's T-tests for pairwise comparisons were used to assess the significance of study factors on GHG emissions (p < 0.05). General linear models were applied to test the form and significance of N application rate on crop yield, N₂O and CH₄ emissions across all available measurements in the compiled dataset. To test the influence of genotype, measurements from genotypes with fewer than three independent replicates were excluded to ensure model robustness, resulting in 20 genotypes across 97 observations. To evaluate whether the linear mixed-effects models (LMMs) presented in Table 1 were constrained by dataset size due to the exclusion of genotypes with fewer than three replicates, we tested additional models. These included LMMs with genotypes having ≥2 replicates, multilevel LMMs incorporating genotype as a random effect, and meta-regressions using all available genotypes with constant variance assumptions due to the absence of standard error data. Model performance was assessed using marginal (R²m) and conditional (R²c) R-squared values, with results reported in Supplementary Table 1. The threshold of three replicates per genotype was selected to reduce the risk of overfitting in mixed models. We fitted LMMs using the "lme4" package, with crop genotype and N application rate as fixed effects, and Latitude and Study as random intercepts to account for geographical and experimental heterogeneity. Model selection was based on an increased goodness of fit of the LMMs to the data according to the Akaike Information Criterion (AIC) where ΔAIC was < -2 for each additional degree of freedom.

Results

Environmental and experimental drivers of N₂O emissions

Note that flux data were log-transformed prior to analysis to normalize residuals and stabilize variance. Back-transformed values approximate relative changes (fold differences) rather than absolute changes, which should be considered during interpretation. N₂O-N cumulative fluxes varied significantly among the crops (Figure 2A). Rice exhibited more variable fluxes, while soybean showed the lowest, and maize and wheat exhibited the highest fluxes, respectively. N₂O-N cumulative fluxes measured in field conditions were significantly higher than those from pot experiments (Figure 2B), indicating that pot studies may underestimate field-scale N₂O emissions, possibly due to constrained root growth in pots or altered microclimate effects. There was no statistically significant difference in N₂O-N cumulative fluxes between open-system and closed-system chambers, suggesting that chamber design does not bias overall emission estimates in our dataset (Figure 2C). No significant difference was observed across MAT categories (<10°C, 10–20°C, >20°C), indicating that temperature alone may not be a strong forecaster of N₂O-N cumulative fluxes (Figure 2D). However, N₂O-N cumulative fluxes were significantly influenced by MAP groups,

TABLE 1 Summary of linear mixed effect model results, testing the influence of N application rate and genotype on N₂O emissions, CH₄ emissions and crop yield as fixed effects.

N ₂ O emissions (kg ha ⁻¹) (N=47)	Df	R ² m	R ² c	AIC	ΔAIC _{df}
Null	4	0	0.654	61.61	0
+ N Application Rate	5	0.720	0.807	33.93	-27.69
+ Genotype	18	0.827	0.890	52.54	NS
CH ₄ emissions (kg ha ⁻¹) (N=57)					
Null	4	0	0.565	524.07	0
+ N Application Rate	5	0.095	0.459	526.95	NS
+ Genotype	19	0.788	0.809	390.51	-8.35
Crop Yield (N=49)					
Null	4	0	0.442	826.06	0
+ N Application Rate	5	0.030	0.476	822.91	-3.16*
+ Genotype	16	0.703	0.725	646.05	-16.08

Latitude and study were used as random effects. The final models for all variables are presented in Supplementary Table 3. NS indicates that the specific term was not selected (ΔAIC_{df} > 2). *indicates that the specific term is no longer significant when the second fixed effect was accounted for.

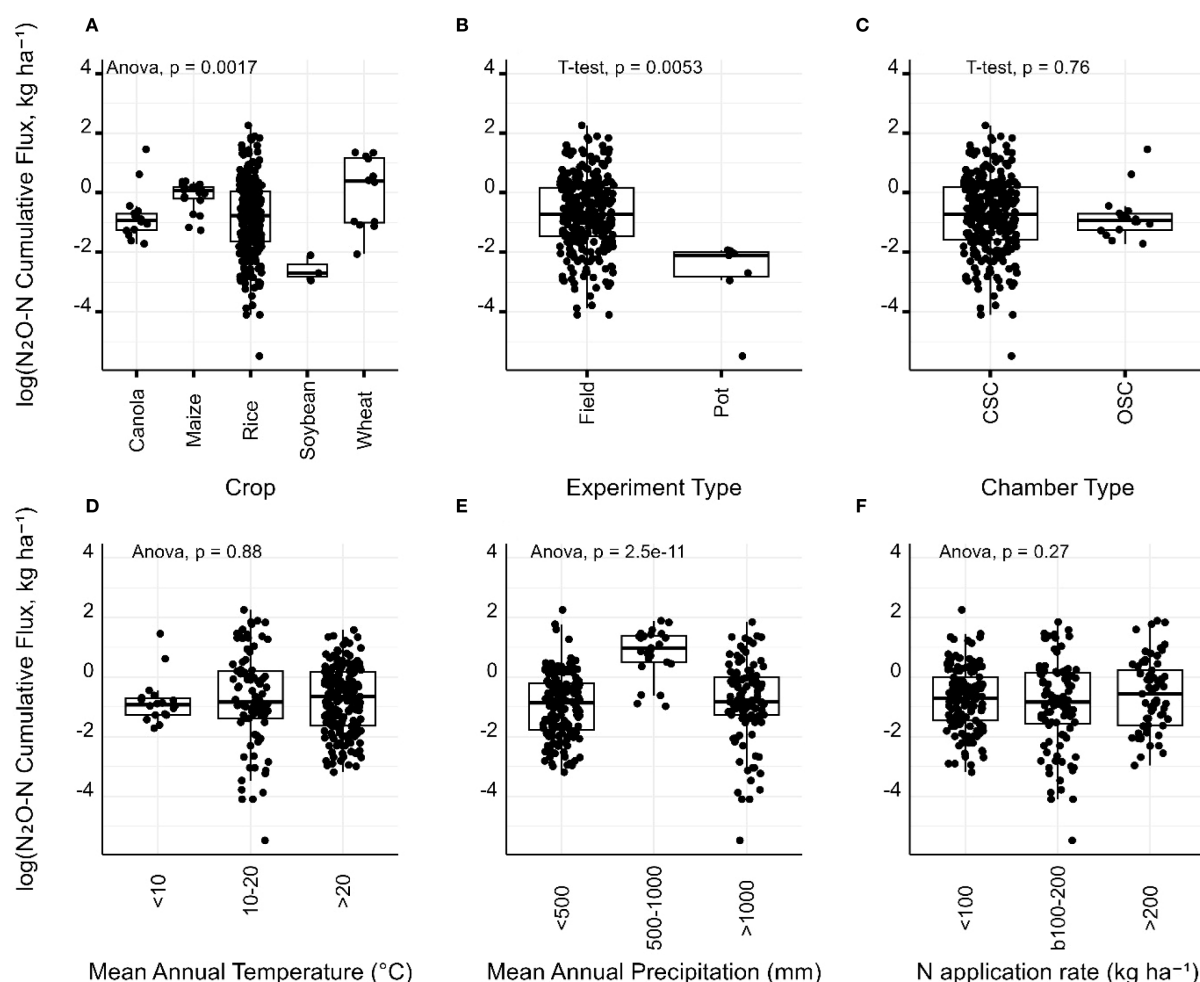


FIGURE 2
Boxplots showing variation in log-transformed cumulative N_2O -N fluxes across (A) crop types, (B) experimental setting (field vs. pot), (C) chamber type (closed system chamber (CSC) vs. open system chamber (OSC)), (D) mean annual temperature (MAT), (E) mean annual precipitation (MAP), and (F) nitrogen fertiliser application rate. Anova and t-test p values indicate significance levels between groups, and boxes represent interquartile ranges, horizontal lines indicate medians and symbols denote individual data points. Flux data was log-transformed to normalise residuals and stabilise variance.

particularly between moderate precipitation conditions (500–1000 mm) compared to dry regions (<500 mm) and wetter regions (>1000 mm) (Figure 2E), suggesting that moderate moisture levels may support microbial activity leading to greater N_2O emissions. Surprisingly, no significant difference was observed among N application rate groups (<100, 100–200, >200 kg ha^{-1}), suggesting that the relationship between N input and emissions may be nonlinear or masked by crop-specific or environmental interactions (Figure 2F).

Yield and emissions efficiency relative to nitrogen application rates

Crop yield and yield-adjusted GHG emissions were explored across different N application rate groups (Figure 3). Crop yield

enhanced significantly with increasing nitrogen fertilisation, although no increase was observed between 100–200 and >200 kg N ha^{-1} (Figure 3A). The <100 kg N ha^{-1} group produced the lowest yields, suggesting a yield-limiting nitrogen deficit in many low-input trials. No significant difference was observed for CH_4 -C cumulative fluxes across N application rates (Figure 3B), similar to N_2O -N cumulative flux responses (Figure 2F). Yield-scaled N_2O fluxes (Figure 3C) and CH_4 emissions (Figure 3D), however, did show a significant response to N application rates. Yield-scaled N_2O emissions decreased significantly with increasing N fertiliser input (Figure 3B). The <100 kg N ha^{-1} group exhibited the highest emissions per unit of yield compared to sharply lower values in the 100–200 and >200 kg N ha^{-1} groups. Conversely, yield-scaled CH_4 emissions increased significantly with N application rate, although no measurements were available for the low (<100 kg ha^{-1}) N application group (Figure 3D).

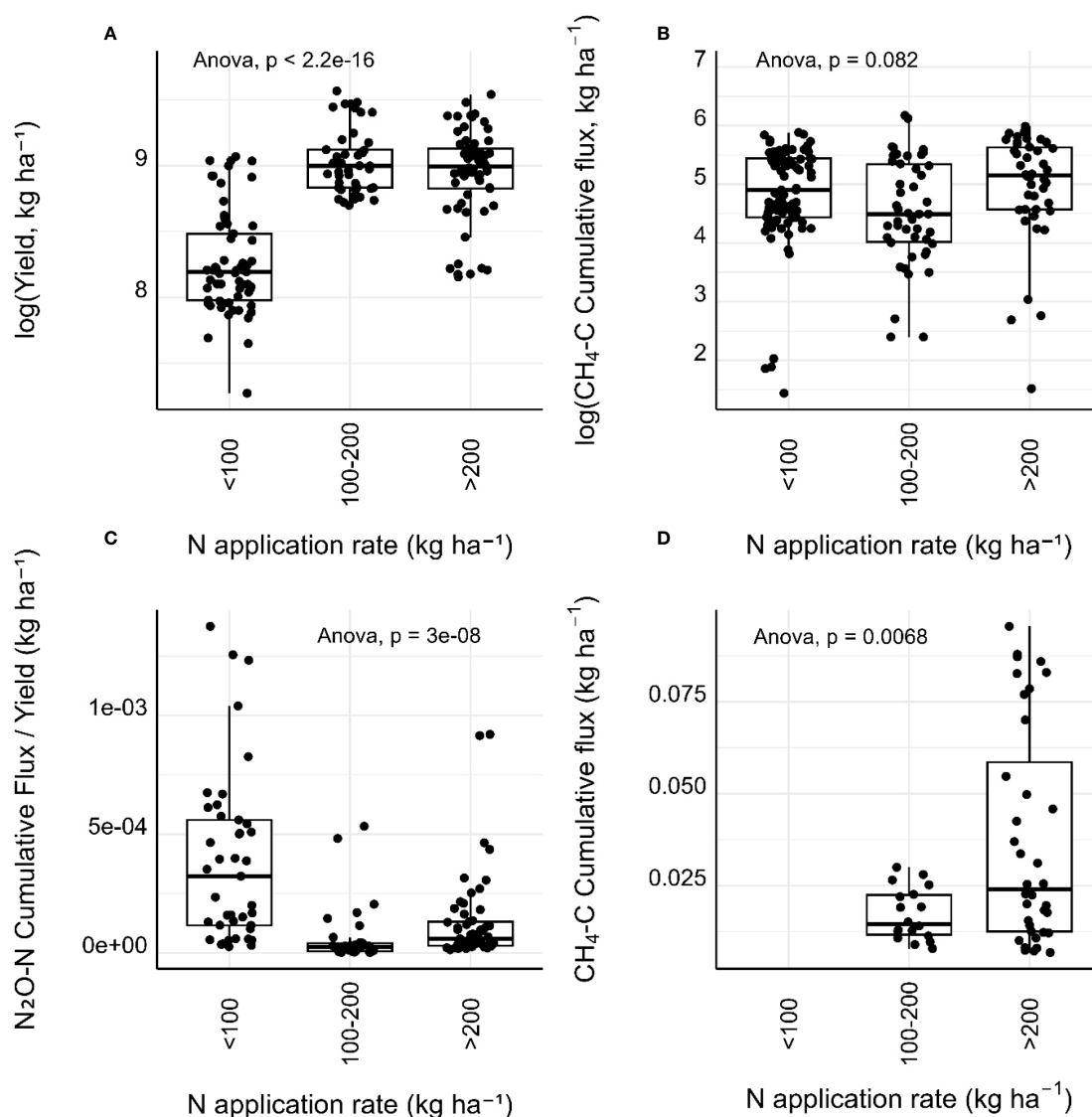


FIGURE 3

Boxplots showing (A) log-transformed crop yield (kg ha^{-1}), (B) cumulative $\text{CH}_4\text{-C}$ emissions, (C) cumulative $\text{N}_2\text{O-N}$ emissions per unit yield, and (D) cumulative $\text{CH}_4\text{-C}$ emissions per unit yield, across nitrogen application rate groups. Anova p values indicate significance levels between groups, and boxes represent interquartile ranges, horizontal lines indicate medians and symbols denote individual data points. Flux data was log-transformed to normalise residuals and stabilise variance.

Relationships between crop yield, GHG emissions and nitrogen application

Regression analyses examining the relationships between N fertilisation rate with N_2O emissions, crop yield, and CH_4 emissions revealed different N responses (Figure 4). N_2O emissions increased exponentially with nitrogen application rate, showing a strong nonlinear relationship (Figure 4A, adjusted $R^2=0.284$, $p < 0.0001$). Crop yield exhibited a curvilinear response to nitrogen input (Figure 4B, $R^2=0.158$, $p < 0.0001$), peaking around $180\text{--}200 \text{ kg N ha}^{-1}$. Below this threshold, yields increased steeply with added N, while beyond this threshold yield gains diminished or plateaued. CH_4 emissions also increased with nitrogen application,

though the relationship was weaker than for N_2O and yield (Figure 4C, adjusted $R^2=0.159$, $p < 0.0001$).

Influence of N application and genotypic variation on GHG emissions and crop yield

Twenty genotypes, with at least three replicates each, were recorded in our dataset ($N=97$). We applied LMMs to the filtered genotype dataset, with latitude and study as random effects, and tested null models against models with N application rate and genotype as fixed effects (Table 1). When this dataset was further filtered to include available measurements for N_2O emissions and

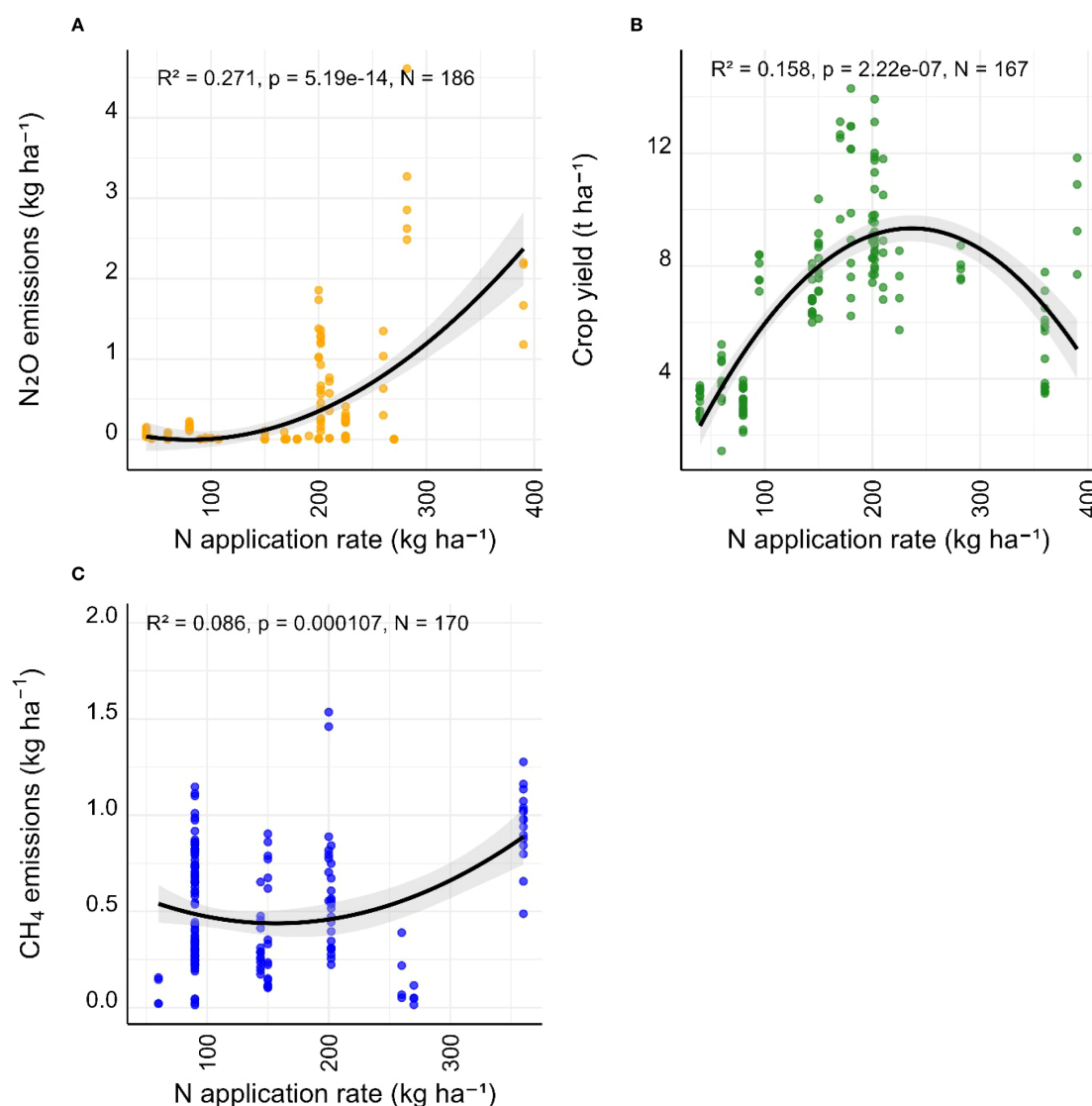


FIGURE 4

Regression relationships between nitrogen application rate (kg ha⁻¹) and: (A) N₂O emissions, (B) crop yield (t ha⁻¹), and (C) CH₄ emissions. Each panel shows fitted regressions with 95% confidence intervals (grey shading). Statistical parameters from the model fits are shown in each panel.

crop yield with N application rate measurements, $n=47$, $n=57$ and $n=49$ measurements were available to fit the N₂O, CH₄ and crop yield models, respectively. Selected models, based on goodness of fit and model parsimony, included N application rate for N₂O and crop yield, and genotype effect for CH₄ and crop yield (Table 1). All models showed good explanatory power of the fixed effects ($R^2_m=0.720$, $R^2_m=0.788$, $R^2_m=0.703$). However, while N application rate explained much of the variation in N₂O emissions ($\Delta AIC_{df}=-27.69$), genotype variation had a much greater explanatory power for CH₄ ($\Delta AIC_{df}=-8.35$) and crop yields ($\Delta AIC_{df}=-16.08$, Table 1).

Observed and predicted values from the best-fitting LMMs for N₂O emissions and crop yield are compared in Figure 5. Comparison of the LMMs in Table 1 with alternative models, including those with genotypes having ≥ 2 replicates, multilevel LMMs with genotype as a random effect, and meta-regressions,

did not indicate a consistent improvement in explanatory power for N₂O emissions (Supplementary Table 1). For N₂O, the original model with ≥ 3 replicates yielded the highest conditional R-squared, suggesting robust capture of variance by fixed and random effects. In contrast, the explanatory power for CH₄ flux improved with dataset size, with the LMM including genotypes with ≥ 2 replicates achieving higher marginal R-squared, indicating a stronger influence of genotype when more data were included. For crop yield, the original models maintained high explanatory power, with minimal gains from alternative approaches. Meta-regressions, limited by constant variance assumptions, provided limited additional insight due to convergence issues for N₂O and yield.

The observed clustering of many genotypes near the x-axis and below the 1:1 line for N₂O predictions (Figure 5A) suggests the model tended to underpredict higher N₂O values, particularly in genotypes or contexts with elevated emissions. In comparison,

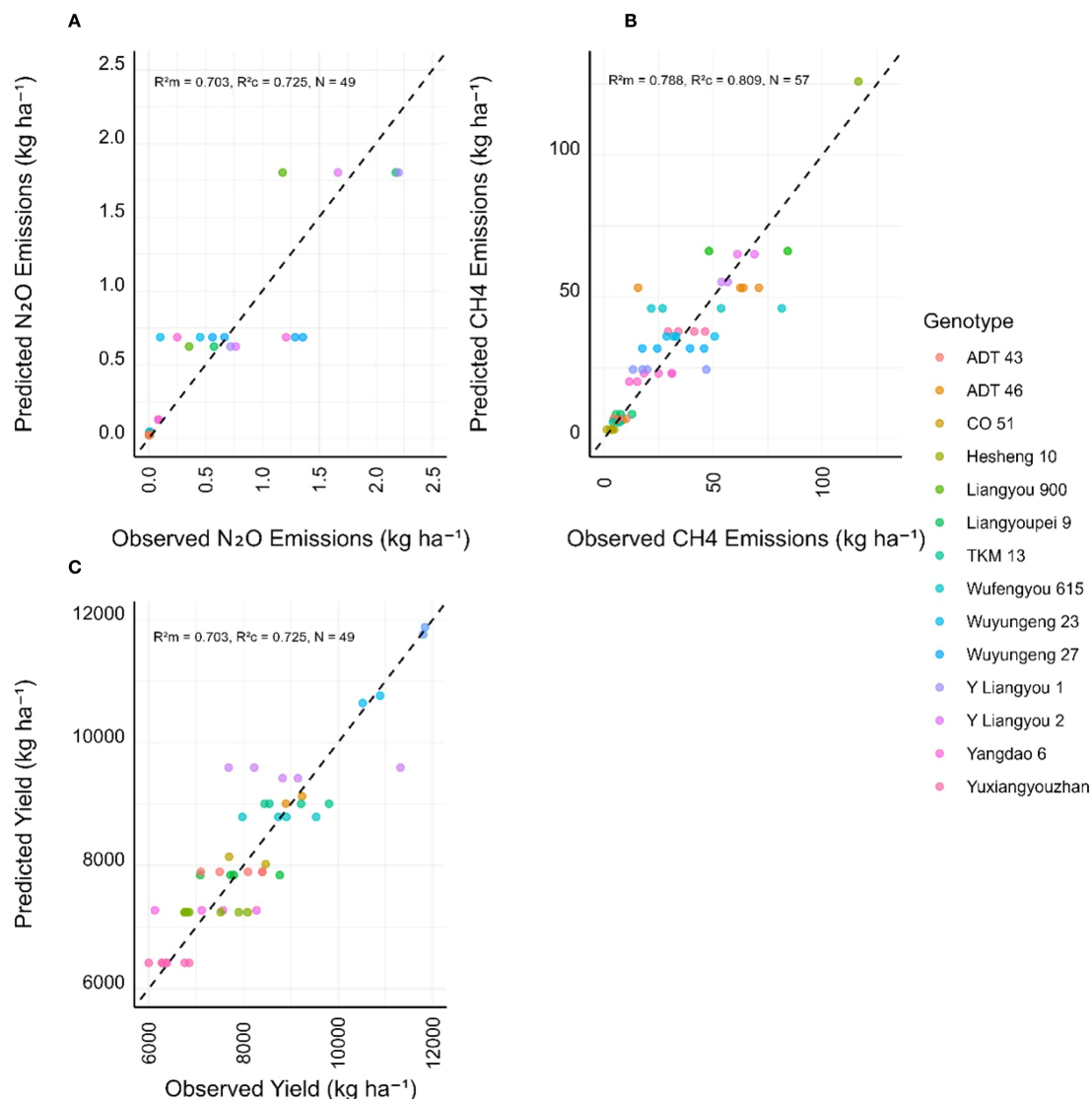


FIGURE 5

Predicted vs observed (A) N₂O emissions, (B) CH₄ emissions and (C) crop yield for the best fitting LMMs identified in Table 1. Dashed lines represent a perfect 1:1 fit, and marginal and conditional R^2 values are shown. Random effects in the models were latitude and study for all variables, with (A) N application rate, (B) N application rate and genotype and (C) genotype selected as fixed effects. Symbol colour represents different genotypes.

predictions for CH₄ (Figure 5B) and crop yield (Figure 5C) were more tightly aligned along the 1:1 line and together with Table 1 suggests that genotypic differences meaningfully capture variability in both response variables.

Discussion

Our global synthesis highlights the complexity of factors influencing N₂O and CH₄ emissions from widely grown cereal and oilseed cropping systems, particularly under variable N fertilisation regimes. While environmental variables such as MAP and experimental setting explained a substantial portion of the variability in cumulative N₂O fluxes (Figure 2), N application rate effects were more apparent when fluxes were scaled by crop yield

(Figure 3). Across crops, N₂O emissions increased exponentially with N fertiliser rate and this trend is consistent with previous meta-analysis studies examining the response of N₂O emissions to N fertiliser rate (Guo et al., 2022; Shcherbak et al., 2014). Crop yield followed a saturation curve, and CH₄ emissions showed a weaker but significant positive trend with increasing nitrogen inputs (Figure 4). Given the prevalence of rice systems in our dataset, however, these patterns likely reflect conditions typical of flooded paddy cultivation. Across genotypes with sufficient replication, we found that while genotype has a pronounced effect on CH₄ emissions and crop yield, the role of genotypes in explaining N₂O emissions is comparatively limited, with emissions primarily driven by fertiliser rate and contextual factors (Figure 5) (Hansen et al., 2019). Genotype had a strong effect on CH₄ but not N₂O, likely because CH₄ flux is strongly plant-mediated via root aerenchyma

development, radial oxygen loss, and exudates, which vary markedly between genotypes. By contrast, N₂O emissions are more tightly coupled to soil microbial processes (nitrification/denitrification) and strongly masked by environmental drivers (moisture, N input), thereby obscuring genotype effects. Research shows stronger genotype effects on N₂O only under controlled or single-site studies, suggesting environment × genotype interactions are key (Chen et al., 2021; Peyrard et al., 2016). These biases in our dataset (overrepresentation of rice and temperate regions) likely amplify genotype effects on CH₄ in flooded systems while limiting detection of N₂O effects in uplands. Our findings reinforce the need for mitigation strategies in global croplands that integrate genetic, environmental, and management dimensions, and the need to address several research gaps for more comprehensive analyses of genotypic effects on crop GHG emissions, including an improved understanding of the underlying physiological and microbial mechanisms.

Several plausible mechanisms may underlie the influence of crop genotype on N₂O emissions (Baggs et al., 2023). Genotypic differences in root morphology and architecture can influence N uptake, soil aeration, and microbial habitat conditions, thereby regulating the balance between nitrification and denitrification. Root exudates and rhizosphere pH modification may also alter microbial community composition and activity, further contributing to variation in fluxes (de Klein and Di, 2018). Differences in nitrogen assimilation efficiency and senescence traits may additionally affect the timing and magnitude of N₂O release (Wingler and Soualiou, 2025). Future research should investigate these mechanisms in interdisciplinary studies combining plant physiology and soil microbial ecology (Philippot et al., 2009).

Environmental and experimental context effects

Cumulative N₂O emissions varied widely across crop types and experimental settings (Figure 2), with rice exhibiting lower emissions than maize or wheat, consistent with differences in aeration, soil moisture, and denitrification potential between flooded and upland systems. In contrast to rice systems, oilseed studies in our dataset reported either neutral or slightly positive CH₄ fluxes. This is consistent with evidence that nitrogen fertilisation can suppress methane oxidation, thereby reducing the soil sink capacity (Sun et al., 2016). Such dynamics highlight the need for broader research beyond rice, particularly in upland systems where methane oxidation plays a larger role in net fluxes. The absence of a clear temperature effect but significant differences across precipitation categories suggests that water availability may be a more direct driver of microbial N₂O production than temperature in these systems, which could be further influenced by approximately 80% of our dataset consisting of genotypes grown in flooded rice paddies. Prior studies have suggested that soil moisture is a key driver of N₂O production predominantly through control of nitrification and denitrification (Butterbach-

Bahl et al., 2013; C. Wang et al., 2021), however these studies have also emphasised how temperature influences N₂O production. Additionally, the higher emissions observed under field conditions compared to pot studies should be considered when pot trial datasets are used to estimate field-scale GHG dynamics.

Interestingly, differences in N₂O-N emissions across N application groups were not statistically significant (Figure 2F), but more significant relationships were detected by weighting fluxes by crop yield (Figure 3). Regression models demonstrate a non-linear, exponential increase in N₂O with increasing N input (Figure 4A), a finding that aligns with prior meta-analyses (Guo et al., 2022; Shcherbak et al., 2014). This non-linearity is often amplified under wet soil conditions where denitrification dominates, leading to higher N₂O fluxes (Girkin and Cooper, 2022; Stehfest and Bouwman, 2006). Such environmental modulation may also obscure genotype-level effects, suggesting that genotyped-based mitigation of GHG emissions will be most effective when combined with optimised N management strategies.

Trade-offs between yield and GHG emissions

Crop yield increased with nitrogen input as expected (Figure 3A), but diminishing returns were evident beyond ~200 kg N ha⁻¹ (Figure 4B), consistent with known saturation effects (Singh, 2024; Biswas and Ma, 2016; Sun et al., 2020). Importantly, emissions per unit yield, an indicator of NUE, declined significantly with moderate N inputs (Figures 3C, D), suggesting an emissions-efficiency threshold in the 100–200 kg N ha⁻¹ range. This result supports repeated calls to optimise, rather than maximise, N application rates to balance productivity with environmental sustainability (McLellan et al., 2018).

A disproportionate acceleration of N₂O emissions as N fertiliser rate exceeded crop uptake capacity was observed (Figure 4A) and this was likely due to increased nitrification and denitrification activity as the excess N fertiliser acts as a substrate for these processes (Long et al., 2021; Ma et al., 2023). A similar response of CH₄ emissions suggests nitrogen-induced shifts in soil redox conditions or crop-mediated CH₄ dynamics, particularly in anaerobic cropping systems like rice (Figure 4C). The curvilinear response of crop yield to N application rate in Figure 4B reflects diminishing returns at high N inputs and indicate over-fertilisation in some systems, a finding which is consistent with what has already been described previously (Hu et al., 2022; Song et al., 2022).

Genotypic effects on GHG emissions and yield

Our LMMs revealed contrasting roles of species genotypes in explaining N₂O emissions, CH₄ emissions and crop yield. For N₂O emissions, inclusion of genotype effects in the model did not significantly improve fit ($\Delta AIC = -18.6$), and explained variance was largely captured by nitrogen input and study-level random effects

(Figure 5A). This suggests that genotype might influence N_2O emissions, however, those effects are obscured by environmental variability and methodological heterogeneity across the investigated studies. This can be seen when comparing separate datasets from individual studies which suggested that N_2O emissions were affected directly by genotypic variation (Chen et al., 2021; Ma et al., 2012), primarily due to different genotype's effects on soil organic carbon, the soil microbial community and a crop's NUE (Chen et al., 2021; Gogoi and Baruah, 2012; Manco et al., 2024). On the contrary, others suggested that N_2O emissions were not influenced by the genotypic variation (Phungern et al., 2023; Z.-H. Wang et al., 2021) but instead were primarily affected by other factors such as nitrogen application rate, water management or tillage type (Feng et al., 2021; Oo et al., 2018; Zhao et al., 2024). By contrast, we found genotype to have a large effect on CH_4 emissions (Figure 5B) and crop yield (Figure 5C). Genotypic effect on CH_4 can occur for several reasons, including varying root biomass and root radial oxygen loss (Qi et al., 2024) as well as special genotypes which develop larger aerenchyma tissues which facilitate CH_4 transport from the soil to the atmosphere (Kludze et al., 1993). Many of the analysed datasets used for this study concluded that genotypic variation indeed does have an effect on CH_4 emissions (Ding et al., 2022; Kou et al., 2018; Satpathy et al., 1998). Selecting genotypes for improved crop yield has been discussed extensively within the literature (Bailey-Serres et al., 2019; Stella et al., 2023), with greater resistance to disease and pests as well as greater NUE being cited as key factors for greater crop yield (Gaju et al., 2011; Tooker and Frank, 2012).

Implications for climate-smart breeding and future research needs

Taken together, our study demonstrates that N_2O emissions are primarily driven by N input rate, while CH_4 emissions are more genotype-driven. This highlights the importance of yield-weighted emissions as a breeding metric to balance mitigation with productivity. Breeding for low-emission genotypes may benefit from prioritising yield-weighted emissions as selection criteria, particularly under moderate N inputs where genotypic differentiation is more pronounced (Chen et al., 2021; Das and Kim, 2024). At present, we also largely lack an integrated and mechanistic understanding of all the processes by which plants regulate the soil environment, and thus the production and emissions of CH_4 and N_2O (Cooper et al., 2024; Snyder et al., 2009).

Future work should prioritise standardised, multi-genotype field trials of various crops that control for environmental confounders, and thus support development of new tools and models to better elucidate pathways and processes. Such experimental designs would improve detection of subtle genotypic effects on GHG emissions and facilitate integration of GHG emissions related traits into conventional or precision breeding pipelines. Such studies will also enhance global synthesis studies, by resolving critical data gaps and sampling biases that are present within this study, such as crop variety, location bias and crop treatment.

Limitations

A key limitation is the reliance on static chamber measurements in most studies, which may miss episodic N_2O events and underestimate total fluxes. Future work should prioritize automated chambers for higher-resolution data, standardised trial protocols, harmonised GHG reporting and increased multi-crop coverage. Furthermore, our dataset reflects the current evidence base, with a heavy bias toward rice systems (35 of 42 studies) and temperate climates, limiting generalizability to other crops and regions. This overrepresentation likely amplifies detected genotype effects on CH_4 (prevalent in flooded rice systems) while constraining insights into N_2O in upland systems. Findings are thus most robust for rice and temperate zones, underscoring the urgent need for broader crop coverage and multi-location trials.

Conclusion

This global synthesis provides evidence that N application rates are primary drivers for N_2O , with an exponential increase in emissions and a critical inflection point where emissions rise sharply with greater N inputs. A limited direct effect of genotype was found on absolute N_2O emissions, whereas genotype was a significant explanatory variable for CH_4 emissions and crop yield. Focus on yield-weighted emissions rather than absolute emissions is key to developing genotypes that mitigate GHGs while optimizing productivity. For CH_4 , water management and soil carbon (not studied here) are major drivers alongside genotype. The biases in the current dataset, particularly the overrepresentation of rice and temperate climate studies, underscore a critical need for globally coordinated research efforts, such as multi-location trials with a standardized set of diverse genotypes, to provide robust, balanced data for more definitive conclusions.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding authors.

Author contributions

CW: Investigation, Visualization, Software, Data curation, Validation, Writing – review & editing, Formal Analysis, Conceptualization, Methodology, Writing – original draft, Project administration. NG: Funding acquisition, Supervision, Writing – review & editing, Resources, Methodology, Conceptualization, Project administration. ZK: Methodology, Writing – review & editing, Supervision. AJ: Conceptualization, Resources, Writing – review & editing, Project administration, Data curation, Methodology, Software, Supervision, Formal Analysis.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Generative AI statement

The author(s) declare that no Generative AI was used in the creation of this manuscript.

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fagro.2025.1669002/full#supplementary-material>

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