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Intercropping with legumes in the Congo Basin increases maize yields but not greenhouse gas emissions



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Agricultural intensification on existing arable lands has been proposed to reduce deforestation in the Congo Basin, although the effects of intensification on soil greenhouse gas (GHG) emissions have not yet been investigated. Here, we present the first field study to quantify the trade-offs between yield and GHG emissions across different intensification options in this region. We show that intercropping with nitrogen-fixing beans not only provided additional protein-rich food but also increased maize yields by 1.4-fold while leaving N_2O emissions and the soil CH_4 sink unchanged compared to unfertilized maize. In contrast, a moderate mineral fertilizer application of $66 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ doubled yields, but reduced the soil CH_4 sink strength, and increased N_2O emissions fivefold to about $4 \text{ kg N}_2\text{O-N ha}^{-1} \text{ yr}^{-1}$. These N_2O emissions also exceeded those of natural forests by more than a factor of three, highlighting the GHG cost of mineral fertilizer use in addition to CO_2 emissions from soil organic carbon loss following land conversion. In sum, intercropping with nitrogen-fixing beans had the lowest yield-scaled GHG emissions and can help to address protein malnutrition in regions with limited access to mineral fertilizers or particularly high N_2O emissions.

The forests of the Congo Basin, covering some 200 million hectares, represent one of the world's most important ecological zones, providing habitat for many species and a source of livelihoods for over 75 million people^{1,2}. These forests play an essential role in global climate change mitigation by storing 40 Gt of carbon (C) in tree biomass and in soils³. However, they are threatened by deforestation and land-use change, which occurred at a rate of 0.09% per year between 1990 and 2000, 0.1% between 2000 and 2010^{4,5}, and 0.21% between 2015 and 2020. For the same period (2015–2020), the deforestation rates were 2.1% in the Central African Republic, 0.71% in Congo, 1.46% in the Democratic Republic of Congo, and 0.21% in Gabon⁶. In Cameroon, for example, annual forest cover loss was estimated at 0.18% per year from 2000 to 2010^{7,8}. In contrast to Latin

America, where deforestation is primarily driven by large-scale agricultural expansion⁹, deforestation and land-use change in the Congo Basin are mostly a consequence of small-scale subsistence agriculture, mainly using slash-and-burn techniques^{10–12}. This type of agriculture, characterized by very low productivity on poor soils (due to continuous cultivation without nutrient replenishment) and poor agricultural practices, accounts for more than 80% of the rate of deforestation in the region^{12–14}.

The Congo Basin is experiencing significant human population growth, with an average annual growth rate of 3.6% between 2000 and 2010 and a projected growth rate of 2.2% between 2020 and 2030. This rapid growth is expected to double the region's population between 2000 and 2030, reaching approximately 170 million people¹⁵. Furthermore, the

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population is projected to increase fivefold by 2100¹³. Increasing demand for food to feed the rapidly growing population is expected to put additional pressure on the forests of the Congo Basin. The critical challenge is therefore: How to meet future food demand while halting deforestation?

Agricultural intensification, which focuses on increasing crop yields on land already converted from native ecosystems, offers a promising strategy for increasing food production while reducing pressure on forests^{16–20}. This approach, which is central to the African Green Revolution, involves a range of techniques and practices such as the development and adoption of high-yielding and pest-resistant crop varieties, increased use of fertilizers, mechanization, irrigation technology, and intercropping. In the Congo Basin, where agriculture is predominantly small-scale and often agroecological “by default”^{21,22}, the strategic use of mineral fertilizers and intercropping with nitrogen-fixing legumes are seen as promising ways to increase yields and diversify crop production. Studies have shown that the application of mineral fertilizer significantly increases crop yield. For instance, Guo et al.²³ found that mineral N fertilization increased maize yields by approximately 80% in different climatic regions due to increased soil N availability in the form of ammonium NH_4^+ and nitrate NO_3^- . In contrast, intercropping, the practice of growing two or more crop species together in the same field²⁴, can improve soil fertility and nutrient cycling. N-fixing legumes, when intercropped, can improve soil N availability, thereby supporting the growth of the primary crop and increasing overall productivity through complementarity or facilitation^{25,26}. For example, Agbor et al.²⁷ showed that maize intercropping with N-fixing legumes tripled maize yields in field trials in southern Cameroon.

While agricultural intensification holds promise for addressing food security challenges in the Congo Basin, its impact on greenhouse gas (GHG) emissions, particularly non- CO_2 gases such as nitrous oxide (N_2O) and methane (CH_4), remains to be assessed. Recent measurements from intact forests in the region reveal comparably low N_2O emissions and significant CH_4 sinks, underscoring the importance of preserving forest carbon and nitrogen dynamics^{28,29}. Agriculture was responsible for 13–21% of total global anthropogenic GHG emissions during the period 2010–2019, with N_2O , CH_4 , and CO_2 contributing 46%, 45%, and 9%, respectively^{30,31}. N_2O emissions from agriculture are estimated to be about 3.8 Tg $\text{N}_2\text{O-N yr}^{-1}$ of total anthropogenic N_2O emissions (7.3 Tg $\text{N}_2\text{O-N yr}^{-1}$)³². Given that the 100-year global warming potential of N_2O and CH_4 are 273 and 27.2 times higher, respectively, than those of CO_2 ³³, understanding the impact of agricultural intensification on GHG emissions is critical. With the commitment of Congo Basin countries to reduce emissions from deforestation and forest degradation (REDD+), such research is essential to develop sustainable intensification practices that balance

the need for increased agricultural productivity with the imperative to mitigate climate change.

Maize (*Zea mays* L.) is a staple crop grown throughout Africa, serving as a source of carbohydrates and an essential input for local agro-industries^{34–36}. The African Development Bank (AfDB) has identified maize as a priority crop for increasing agricultural productivity in sub-Saharan Africa³⁷. With the region’s projected population growth, the demand for maize is expected to increase accordingly. In response to this anticipated demand surge, we investigated two maize intensification strategies: intercropping with nitrogen-fixing beans and the application of mineral N fertilizer to typically low-productivity forest margin fields in Cameroon. Our study aimed to assess the impact of these intensification practices on (1) maize grain yield and (2) soil-atmosphere exchange of GHGs (N_2O , CH_4 , and CO_2), using an adjacent secondary forest (SF) as a baseline for GHG fluxes. Finally, we aimed to provide yield-scaled non- CO_2 GHG fluxes associated with maize intensification options, thereby providing scientific evidence for sustainable maize cultivation on the Congo forest margins.

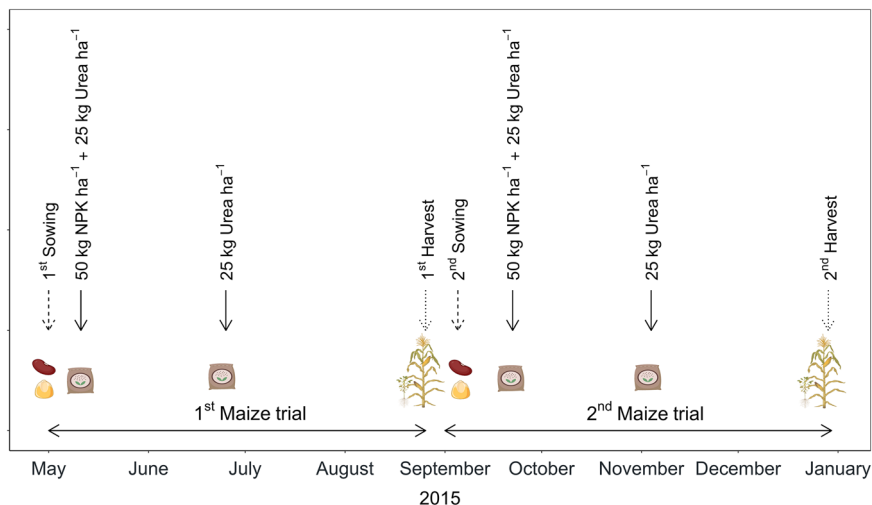
Results

Here we report results from a field experiment conducted over two consecutive maize growing seasons in 2015 to evaluate three maize cultivation practices: (1) unfertilized maize control (MC), (2) maize fertilized with mineral nitrogen at 66 kg N $\text{ha}^{-1} \text{yr}^{-1}$ (MF), and (3) maize intercropped with N-fixing beans (MB). Additionally, a nearby secondary forest (SF) was monitored throughout the study period to serve as a baseline for GHG fluxes. The first maize season spanned from sowing on May 1 to harvest on August 26, while the second season ran from sowing on September 5 to harvest on December 29 (Fig. 1).

Total plant biomass and maize grain yield

Total plant biomass (maize grains, beans, stems, cobs, and residues) increased significantly with both the incorporation of beans and with mineral N fertilization ($p < 0.001$). The average biomass for MC was the lowest at 7.2 ± 0.6 metric tons (t) ha^{-1} (Fig. 2A). Intercropping with beans significantly increased biomass to 10 ± 0.9 t ha^{-1} . The mineral fertilizer (MF) treatment resulted in the highest increase in productivity by more than doubling biomass to 15.5 ± 0.6 t ha^{-1} . This significant increase underscores the benefits of mineral nitrogen for plant growth. Maize grain yield followed a similar trend, with the MC treatment showing the lowest yield at 3.6 ± 0.3 t ha^{-1} (Fig. 2B). Intercropping with beans significantly increased yield to 4.9 ± 0.5 t ha^{-1} . Mineral N application resulted in the highest grain yield of 7.7 ± 0.3 t ha^{-1} . During the two maize trials, protein yield increased by approximately 50% in the MB (0.51 ± 0.05 t ha^{-1}) and doubled in the MF (0.73 ± 0.003 t ha^{-1}) compared to the MC treatment (0.34 ± 0.03 t ha^{-1}).

Fig. 1 | Timeline of agronomic events during the two maize growing seasons. Schematic showing the sequence and dates of key agronomic events (sowing, nitrogen fertilization, and harvest) for the two consecutive maize growing seasons in this study. Created in BioRender. Kwatcho Kengdo, S. (2026) <https://BioRender.com/m5t7b7f>.



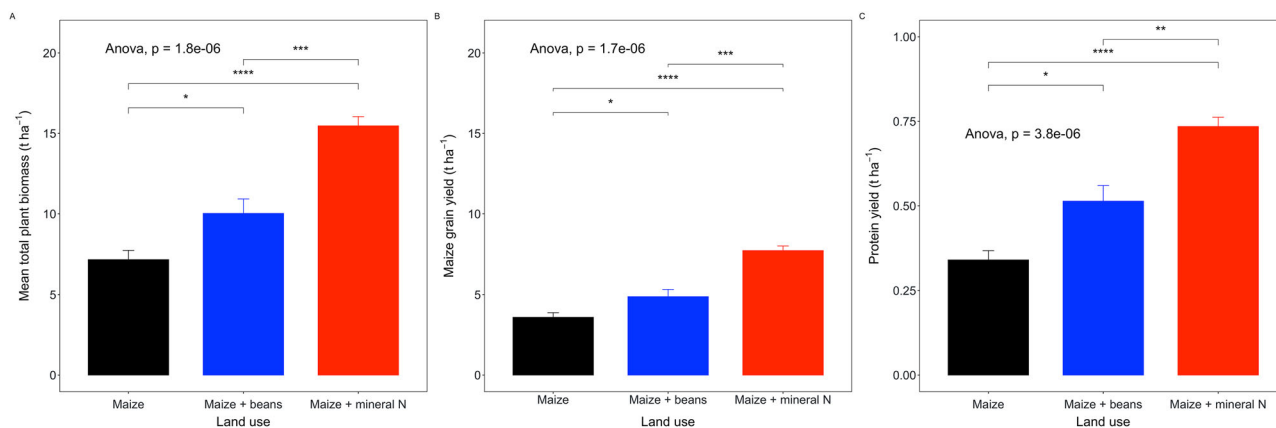


Fig. 2 | Yields of different maize cultivation. Mean total plant biomass (A) maize grain yield (B) and protein yield (C) (kg ha⁻¹) in the maize control, maize + beans, and maize + mineral N, averaged across the two growing campaigns. Total plant

biomass includes plant stems, cobs, and grains. Significance levels are given as **** $p < 0.0001$; *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$.

Soil atmosphere GHG fluxes across land uses

N₂O fluxes showed a large temporal variation, especially with pronounced peaks in response to N fertilization events (Fig. 3c). The MF treatment had the highest N₂O emissions (mean $76.5 \pm 15.4 \mu\text{g N m}^{-2} \text{h}^{-1}$), with sharp peaks exceeding $500 \mu\text{g N m}^{-2} \text{h}^{-1}$ following nitrogen fertilizer applications in the second maize trial. The peaks in the second maize trial with higher precipitation were significantly larger than in the first trial, resulting in a cumulative flux of $4.01 \text{ kg N ha}^{-1} \text{yr}^{-1}$; in the maize + mineral N treatment ($1720.29 \pm 12.87 \text{ kg CO}_2\text{-eq ha}^{-1} \text{yr}^{-1}$), notably higher than in the other treatments. The MC (mean $12.4 \pm 2.2 \mu\text{g N m}^{-2} \text{h}^{-1}$) and MB (mean $9.8 \pm 1.4 \mu\text{g N m}^{-2} \text{h}^{-1}$) treatments showed similar but more subdued N₂O flux patterns, with cumulative fluxes of $0.83 \pm 0.004 \text{ kg N ha}^{-1} \text{yr}^{-1}$ ($356.07 \pm 1.72 \text{ kg CO}_2\text{-eq ha}^{-1} \text{yr}^{-1}$) and $0.62 \pm 0.002 \text{ kg N ha}^{-1} \text{yr}^{-1}$ ($265.98 \pm 0.85 \text{ kg CO}_2\text{-eq ha}^{-1} \text{yr}^{-1}$), respectively. In comparison, the SF showed consistently high N₂O emissions ($21.2 \pm 2.2 \mu\text{g N m}^{-2} \text{h}^{-1}$), with cumulative fluxes of $1.35 \pm 0.004 \text{ kg N ha}^{-1} \text{yr}^{-1}$ ($579.15 \pm 1.72 \text{ kg CO}_2\text{-eq ha}^{-1} \text{yr}^{-1}$).

Net CH₄ fluxes at the soil-atmosphere interface were persistently negative, particularly in the MC and SF treatments, where the flux averaged $-37.5 \pm 2.5 \mu\text{g C m}^{-2} \text{h}^{-1}$ and $-39.6 \pm 3.6 \mu\text{g C m}^{-2} \text{h}^{-1}$, respectively (Fig. 3E). Occasional CH₄ emissions in the MC, MB, and MF treatments (range: $7.55\text{--}24.77 \mu\text{g C m}^{-2} \text{h}^{-1}$) were related to wet soil conditions after rainfall events. Cumulative fluxes in all treatments were relatively similar, with the lowest mean net CH₄ sink strength of about $2 \text{ kg CH}_4\text{-C ha}^{-1} \text{yr}^{-1}$ being observed for soils of the fertilized treatment, and significantly higher CH₄ sink strength of about $2.5 \text{ kg C ha}^{-1} \text{yr}^{-1}$ for soils of the unfertilized control and intercropped treatments. This corresponded to a CO₂ equivalent of $-87.04 \pm 0.18 \text{ kg CO}_2\text{-eq ha}^{-1} \text{yr}^{-1}$ and $-89.94 \pm 0.22 \text{ kg CO}_2\text{-eq ha}^{-1} \text{yr}^{-1}$, respectively. Thus, the soil CH₄ sink strength was 3–23.1 times lower than the source strength of N₂O emissions when expressed as CO₂ equivalents.

Soil respiration varied considerably among the different land use systems (Fig. 3D and Table S2). The SF consistently exhibited the highest CO₂ fluxes, peaking at approximately $266.12\text{--}318 \text{ mg C m}^{-2} \text{h}^{-1}$, especially during the rainy season. In contrast, the CO₂ fluxes in the MC, MB, and MF treatments were significantly lower, ranging between $44.70\text{--}209.81 \text{ mg C m}^{-2} \text{h}^{-1}$. Among these, the SF showed the highest cumulative CO₂ flux ($11.84 \pm 0.014 \text{ t C ha}^{-1} \text{yr}^{-1}$), followed by MB ($6.59 \pm 0.013 \text{ t C ha}^{-1} \text{yr}^{-1}$), MC ($6.48 \pm 0.009 \text{ t C ha}^{-1} \text{yr}^{-1}$), and MF ($6.09 \pm 0.008 \text{ t C ha}^{-1} \text{yr}^{-1}$).

Yield-scaled N₂O emissions

Due to the low importance of CH₄ in the non-CO₂ greenhouse gas balance and the marginal variation of the CH₄ sink among treatments (Table 1), we only scaled N₂O emissions to yields. Yield-scaled N₂O emissions were significantly different between treatments. Yield-scaled N₂O emissions for

the MF treatment averaged about $0.52 \pm 0.02 \text{ kg N}_2\text{O-N per ton of maize grain yield}$, which was significantly higher than the MC treatment alone ($0.24 \pm 0.02 \text{ kg N}_2\text{O-N per ton of maize grain yield}$) and the MB treatment ($0.13 \pm 0.01 \text{ kg N}_2\text{O-N per ton of maize grain yield}$) (Fig. 4A). To provide an alternative perspective that accounts for the nutritional value of the harvest, we also calculated protein-scaled N₂O emissions. These were again highest for the MF treatment ($5.53 \pm 0.22 \text{ kg N}_2\text{O-N per ton of protein yield}$), followed by the MC treatment ($2.51 \pm 0.16 \text{ kg N}_2\text{O-N per ton of protein yield}$), and lowest for the MB treatment ($1.26 \pm 0.12 \text{ kg N}_2\text{O-N per ton of protein yield}$) (Fig. 4B).

Soil and environmental parameters

Mineral soil characterization showed a decrease in SOC concentrations compared to the SF, and slightly increased bulk density values in the crop field in 0–10 cm, while the C:N ratio did not change (Table 2). Still, this resulted in decreased SOC stocks in the crop fields compared to the forest, even though we did not use an equal soil mass approach (a method that corrects for changes in soil bulk density due to compaction³⁸) (Table 2). Specifically, SOC stocks decreased from 26.5 t ha^{-1} to 24.3 t ha^{-1} at 0–10 cm and from 37.4 t ha^{-1} to 29.1 t ha^{-1} at 10–30 cm. Thus, the land-use change induced SOC loss in the upper 30 cm of the mineral topsoil was 10.5 t C ha^{-1} . Soil Ca concentrations were lower in the SF, while P was higher in the maize control (MC) treatment. K concentrations were elevated in both the MC and maize plus beans (MB) treatment.

Soil temperature remained stable throughout, while soil moisture fluctuated significantly with rainfall, being higher during the rainy seasons (April–June and September–November) and lower during the dry season (July–August) (Fig. 3A, B).

Soil mineral nitrogen concentrations

Considering the large differences in N inputs among the maize treatments (0 kg N ha^{-1} in MC vs. $\sim 66 \text{ kg N ha}^{-1}$ in MF), we found surprisingly small differences in NH₄⁺-N and NO₃⁻-N concentrations among the different maize treatments, and also relatively low temporal variability (Fig. S1). Only, the MF treatment occasionally had higher NH₄⁺-N and NO₃⁻-N concentrations, especially after the fertilizer applications (Fig. S1). Overall, we found average NH₄⁺-N and NO₃⁻-N stocks of only about 10–15 kg each across treatments (Fig. S2).

Relationship between GHG fluxes and environmental variables

Nitrous oxide emissions were generally positively correlated with volumetric water content, especially in the MF treatment ($r = 0.55$, $p < 0.001$), which had the highest total N₂O emissions (Fig. 5E and Table 1). The

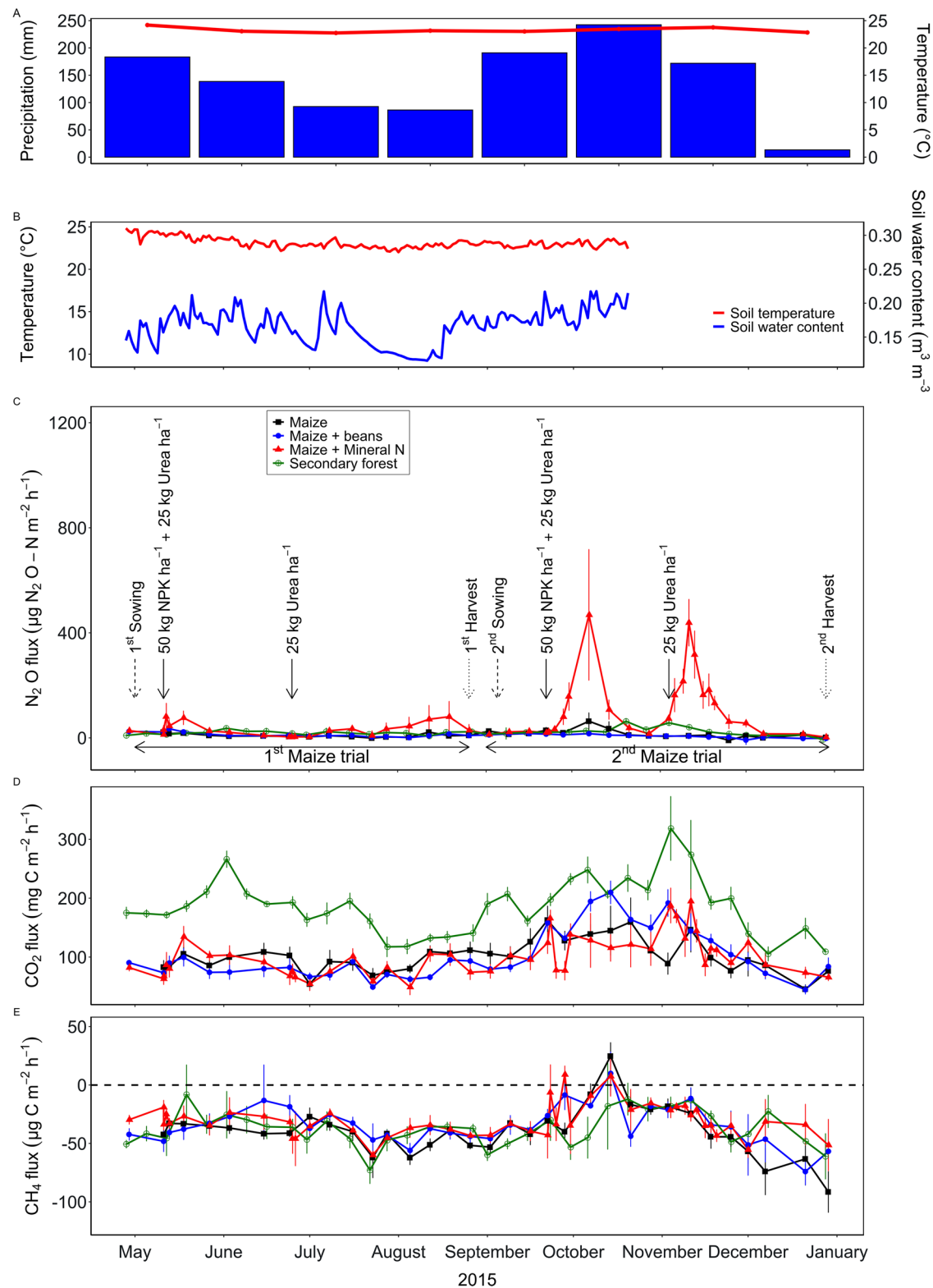


Fig. 3 | Land use effects on soil-atmosphere exchange of greenhouse gases.

Monthly air temperature and precipitation (A); daily soil temperature and soil water content measured in an adjacent mix crop field and representative of the field

conditions across all maize treatments (B); flux of N_2O (C) CO_2 (D) and CH_4 (E) in the secondary forest, maize control, maize + beans, and maize + mineral N. Symbols are mean $\pm$ standard error.

relationship between N_2O emissions and soil temperature was weak and not significant in most treatments, except for a weak positive correlation in the MF treatment ($R = 0.29$, $p = 0.056$, Fig. 5F). The net CH_4 uptake increased with decreasing volumetric water content ($R = 0.77$, 0.69 , and 0.58 for MC, MB, and MF, respectively and Fig. 5C). The relationship between CH_4 flux

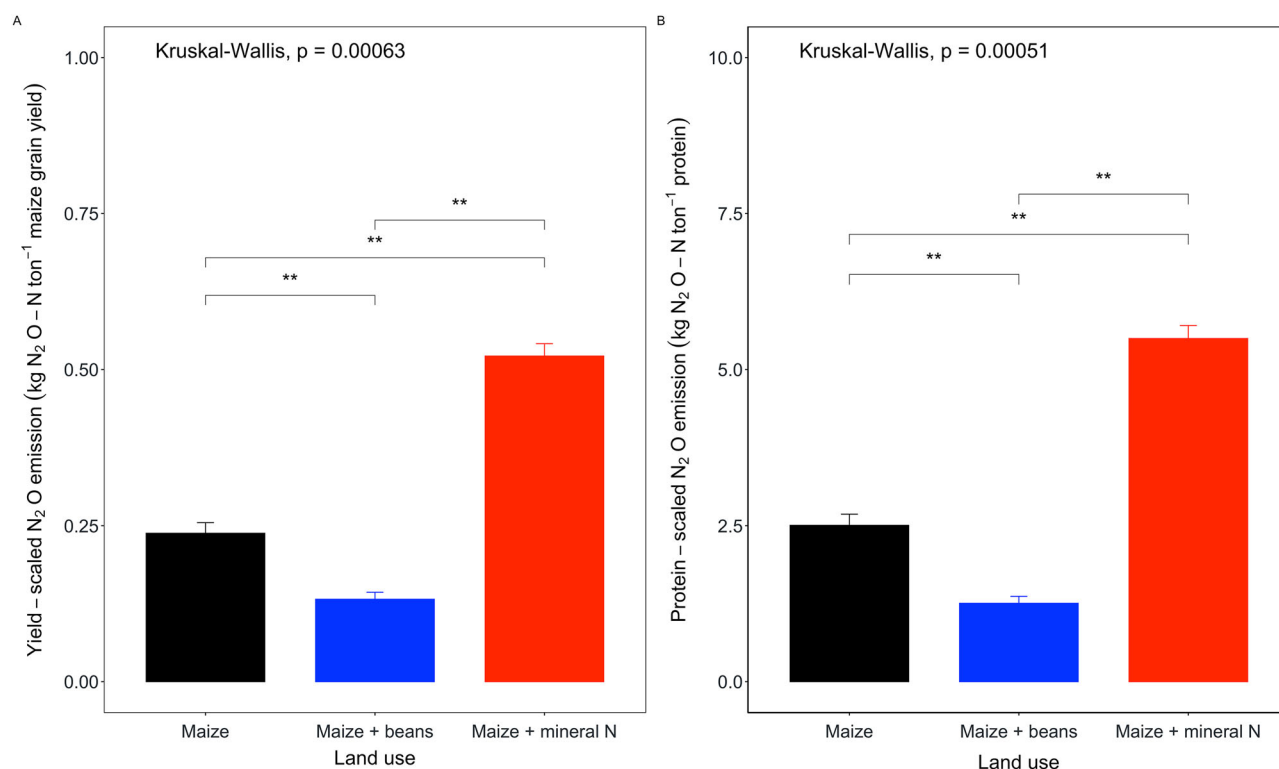
and soil temperature was weaker but positively correlated within the MF treatment ($R = 0.42$, $p = 0.0039$, Fig. 5D).

Soil respiratory CO_2 fluxes were significantly positively correlated with volumetric water content across all treatments (Fig. 5A). The correlation coefficients were highest in the MB and MF treatments

Table 1 | Mean ($\pm$ SE), cumulative fluxes of soil respiration (CO_2), CH_4 , and N_2O , and CO_2 equivalent of non CO_2 gases over the measured period in secondary forest ($n = 4$), maize ($n = 6$), maize + beans ($n = 7$), and maize + mineral N ($n = 7$)

GHG	Land use	Mean $\pm$ SE	Cumulative flux	CO_2 equivalent
CO_2 (R_{soil})		$\text{mg C m}^{-2} \text{ h}^{-1}$	$\text{t C ha}^{-1} \text{ yr}^{-1}$	$\text{kg CO}_2\text{-eq ha}^{-1} \text{ yr}^{-1}$
	Secondary forest	185.3 ± 8.1^b	11.84 ± 0.014^b	-
	Maize	101.5 ± 4.8^a	6.48 ± 0.009^a	-
	Maize + beans	101.7 ± 7.3^a	6.59 ± 0.013^a	-
	Maize + mineral N	101.0 ± 5.0^a	6.09 ± 0.008^a	-
SOC stock change due to forest conversion ($10.5 \text{ t C ha}^{-1} 5 \text{ yr}^{-1}$):				7707
CH_4		$\mu\text{g C m}^{-2} \text{ h}^{-1}$	$\text{kg C ha}^{-1} \text{ yr}^{-1}$	
	Secondary forest	-37.5 ± 2.5^{ab}	-2.40 ± 0.005^a	-87.04 ± 0.18^a
	Maize	-39.6 ± 3.6^a	-2.48 ± 0.006^a	-89.94 ± 0.22^a
	Maize + beans	-34.6 ± 2.8^{ab}	-2.20 ± 0.005^a	-79.79 ± 0.18^a
	Maize + mineral N	-30.8 ± 2.1^b	-2.05 ± 0.004^a	-74.35 ± 0.15^a
N_2O		$\mu\text{g N m}^{-2} \text{ h}^{-1}$	$\text{kg N ha}^{-1} \text{ yr}^{-1}$	
	Secondary forest	21.2 ± 2.2^a	1.35 ± 0.004^a	579.15 ± 1.72^a
	Maize	12.4 ± 2.2^a	0.83 ± 0.004^a	356.07 ± 1.72^a
	Maize + beans	9.8 ± 1.4^a	0.62 ± 0.002^a	265.98 ± 0.85^a
	Maize + mineral N	76.5 ± 15.4^b	4.01 ± 0.03^b	1720.29 ± 12.87^b

Numbers followed by different letters are significantly different. For comparison, we also provide the SOC stock change per year due to forest conversion to cropland as CO_2 equivalent.

**Fig. 4 | Yield- and protein-scaled N_2O emissions across maize cultivation systems. A** Yield-scaled ($\text{kg N}_2\text{O-N t}^{-1}$ maize grain yield) and **B** protein-scaled N_2O emission ($\text{kg N}_2\text{O-N t}^{-1}$ protein) in the maize control, maize + beans, and maize + mineral N across the two subsequent maize trials.

($R = 0.79$, $p < 0.001$, and $R = 0.7$, $p < 0.001$, respectively). Conversely, the correlation between CO_2 flux and soil temperature was less pronounced and varied between treatments (Fig. 5B). While soils from the MB treatment showed a moderate positive correlation ($r = 0.32$), soils from other treatments did not show significant temperature-driven variations in CO_2 flux.

Discussion

Given the expected population growth in the Congo Basin in the coming decades, increasing yields on existing arable lands is urgently needed in order to prevent deforestation. Maize grain yield doubled under mineral N application (7.7 t ha^{-1}), significantly outperforming the maize + beans intercrop (1.4-fold increase: 4.9 t ha^{-1}) and maize control (3.6 t ha^{-1})

Table 2 | Soil characteristics for the different land uses

	Secondary forest		Unfertilized maize control		Maize + beans		Maize + mineral N	
Soil depth (cm)	0–10	10–30	0–10	10–30	0–10	10–30	0–10	10–30
Bulk density (g cm ⁻³)	1.11	1.28	1.25	1.21	-	-	-	-
Porosity (%)	58	52	53	54	-	-	-	-
CEC (cmol ⁽⁺⁾ kg ⁻¹)	6.8 (0.3) ^a	5.6 (0.1) ^a	6.5 (0.2) ^a	5.4 (0.0) ^a	-	-	-	-
C (%)	2.4 (0.1) ^a	1.5 (0.0) ^a	1.9 (0.1) ^a	1.2 (0.0) ^a	-	-	-	-
SOC stocks (t ha ⁻¹)	26.5 (1.0) ^a	37.4 (1.1) ^a	24.3 (1.5) ^a	29.1 (1.0) ^b	-	-	-	-
Total N (%)	0.2 (0.0) ^a	0.1 (0.0) ^a	0.1 (0.0) ^a	0.1 (0.0) ^a	-	-	-	-
C/N	15.2 (0.4) ^a	17.8 (0.4) ^a	16.4 (0.3) ^a	15.7 (0.8) ^a	-	-	-	-
Sand (%)	43.7 (5.5)	-	39.6 (3.5)	-	-	-	-	-
Silt (%)	6.5 (0.0)	-	5.5 (0.1)	-	-	-	-	-
Clay (%)	49.8 (5.5)	-	54.9 (3.6)	-	-	-	-	-
Soil depth (cm)	0–20		0–20		0–20		0–20	
pH (water)	3.8 (0.1) ^b		4.7 (0.3) ^a		4.0 (0.1) ^b		4.1 (0.1) ^b	
pH (KCl)	3.5 (0.1) ^b		4.2 (0.3) ^a		3.7 (0.1) ^b		3.7 (0.1) ^b	
Ca (cmol ⁽⁺⁾ kg ⁻¹)	0.5 (0.1) ^b		4.2 (0.9) ^a		2.1 (0.5) ^{ab}		1.3 (0.4) ^b	
Mg (cmol ⁽⁺⁾ kg ⁻¹)	0.4 (0.1) ^a		0.9 (0.1) ^a		0.6 (0.1) ^a		0.5 (0.1) ^a	
K (cmol ⁽⁺⁾ kg ⁻¹)	0.1 (0.0) ^b		0.2 (0.0) ^a		0.2 (0.0) ^a		0.1 (0.0) ^b	
Na (cmol ⁽⁺⁾ kg ⁻¹)	0.02 (0.0) ^a		0.01 (0.00) ^b		0.009 (0.0) ^b		0.01 (0.0) ^b	
P (μg g ⁻¹)	-		6.8 (2.2) ^a		4.0 (1.0) ^{ab}		1.6 (0.3) ^b	

Different superscript letters indicate a significant difference between treatments ($p < 0.05$).

treatments. Hence, both intensification options can in principle be considered successful in terms of yield increase, with clear advantages for fertilization over BNF-supported yield increases. This substantial yield increase under mineral N application is consistent with the broader literature on the role of mineral N fertilization in increasing crop productivity, especially in nutrient-limited tropical soils³⁹. Maize yield increases due to intercropping with N-fixing beans, relative to unfertilized maize monoculture, have been reported in other studies conducted in Africa^{40–43}. Nitrogen limitation was indicated by persistently low soil mineral N concentrations, illustrating a rapid consumption of applied mineral N fertilizers and N inputs from biological nitrogen fixation. Furthermore, the relatively wide C:N ratio of about 16 supports strong N limitation⁴⁴, as such wide C:N ratios promote the activity of heterotrophic soil microbes, such as denitrifiers, and also heterotrophic microbial N immobilization, so that competition for N between plants and microbes is high⁴⁵, exacerbating N limitation for plants. Thus, the increased N availability due to fertilization has immediate effects on N nutrition of fine roots and leaf growth, leading to higher photosynthetic rates and greater plant biomass production and, ultimately, grain yields⁴⁶. This is also consistent with the increase in total plant biomass under mineral N fertilization in both maize trials (Table S1).

The increase in maize grain yield in the maize + N-fixing beans treatment, although lower than that in the maize + mineral N treatment, emphasizes the importance of BNF in improving N availability, increasing maize N uptake and grain yield⁴⁷. This clearly reduces the need for mineral N fertilizer application and thus has significant potential to help close yield gaps. The amount of N fixed by *Phaseolus vulgaris* L. varied between studies, ranging from 10 to 97 kg N ha⁻¹^{41,48,49}. Although not specifically tested in this study, the mechanisms of N transfer from beans to maize plants may have included rhizodeposition, interspecific root interactions, and decomposition of bean nodules releasing N^{50–52}. Such short-term interactions between N-fixing plants and maize N nutrition seem very likely, given the immediate strong response in maize growth observed in the first cycle of intercropping with N-fixing beans. Beyond biological nitrogen fixation and N-nursing, the intercropped beans may improve maize performance through weed suppression, erosion and leaching control, and improved

ground cover, which helps conserve soil moisture in the surface layer. It also diversifies farmers' income by allowing them to harvest different crops on the same land. Still, we demonstrate that mineral N fertilization provided a larger, more immediately available N input, resulting in a greater maize yield response. Furthermore, the addition of more mineral N fertilizers could result in even significantly higher yields, as the potential maize yields under the studied wet tropical soil conditions could be several times higher than those obtained in our study in the MF treatment⁵³. However, intercropping with N-fixing beans remains a viable alternative for smallholder farmers seeking to increase productivity without relying on external mineral N inputs and their associated cost⁵⁴. This is very relevant for the Congo Basin, where smallholder farmers may have limited access to chemical fertilizers due to their high costs. While intercropping beans requires more complex management and increased labor for tasks such as planting, weed control (especially in the early growing season), and harvesting, it offers significant benefits by providing an additional protein-rich food. Despite the absence of site replication and the limitation to two growing seasons in this pioneering study which requires careful generalization of findings, we demonstrate significant maize grain yield benefits from mineral N fertilizer application and intercropping with N-fixing beans, which are highly relevant to farmers in the Congo basin and can increase food security.

Yield-scaled N₂O emissions are an important indicator as they relate agricultural productivity to GHG emissions^{55–58}. It, therefore, allows the identification of good management or agricultural practices that reduce N₂O emissions while maintaining or increasing crop yields³². The doubling of yields in the maize + mineral N fertilizer treatment was accompanied by a fivefold increase in N₂O emissions. The sharp peaks following fertilizer application, especially during the second maize trial (Fig. 3C), clearly illustrated the role of fertilizer N in regulating N₂O emissions^{59,60}. The cumulative N₂O emissions in this treatment (4.0 kg N ha⁻¹ yr⁻¹) were significantly higher than in the maize intercropped with N-fixing beans (0.62 kg N ha⁻¹) and maize control (0.83 kg N ha⁻¹) treatments (Fig. 6).

While there are no empirical studies from the Congo Basin, relatively few peer-reviewed studies and MSc and BSc theses have reported N₂O emissions from maize fields in the tropical and subtropical regions of Africa

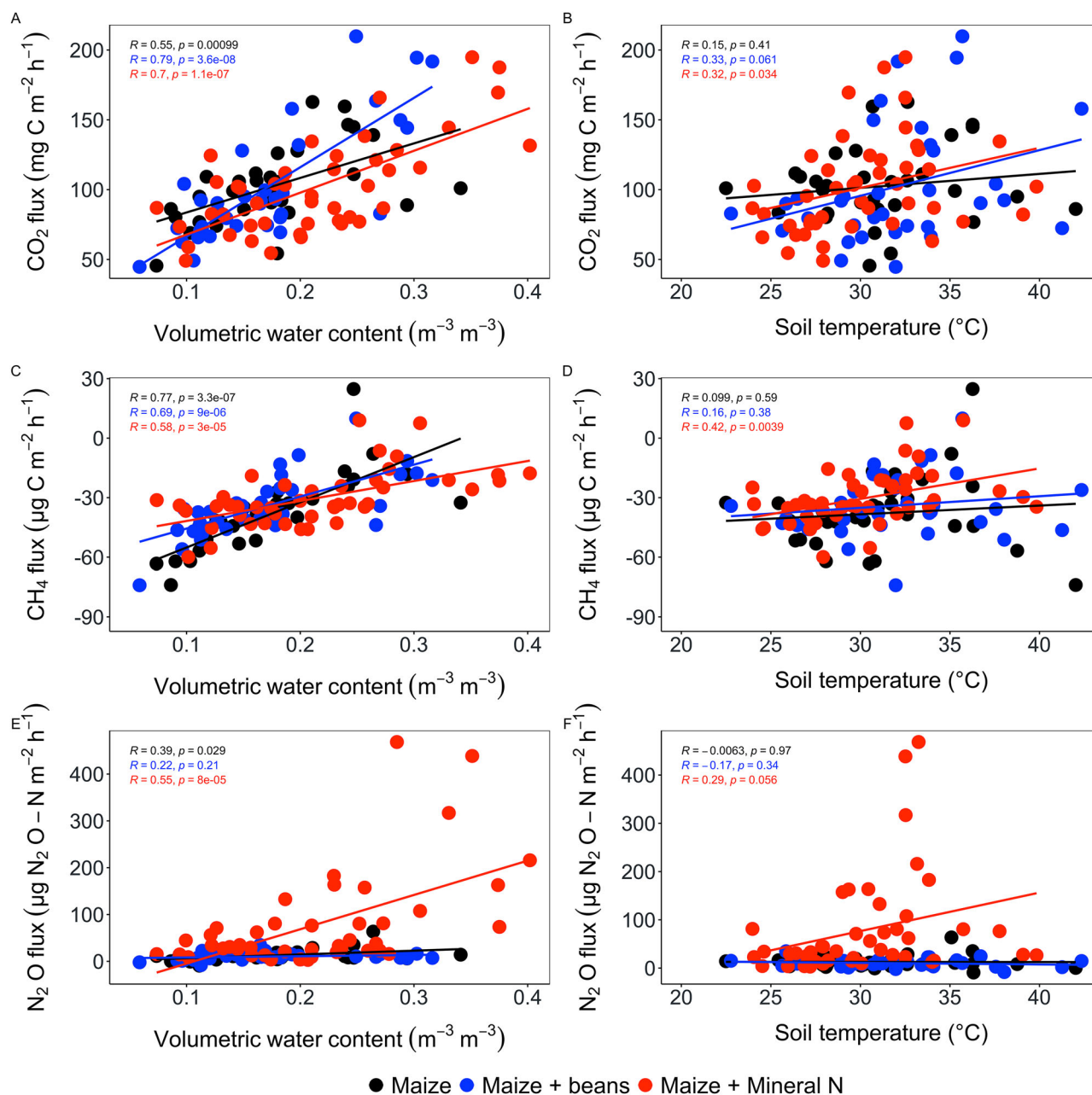


Fig. 5 | Environmental controls of greenhouse gas fluxes. Relationship between CO₂, CH₄, and N₂O fluxes and volumetric soil water content (A, C, E) and soil temperature (B, D, F) in the maize control, maize + beans and maize + mineral N treatments.

and other regions of the world⁵³. The N₂O emissions of 4 kg N ha⁻¹ yr⁻¹ we found in the fertilized treatment are at the very upper end of these reports. At an N application rate of 66 kg N ha⁻¹, the N₂O emission factor is as high as 6%, or 5% when considering background fluxes of 0.8 kg N ha⁻¹ from the MC treatment (emission factor calculated as [(N₂O-N emission from the fertilized treatment) - (N₂O-N emission from the unfertilized control)] / (Rate of N fertilizer applied) × 100). Leitner et al.⁵³ estimated that closing the maize yield gap in sub-Saharan Africa by 75% would require the application of >80–100 kg N ha⁻¹, thereby tripling yields but increasing N₂O emissions even by as much as seven times. In the Congo wet forest region, where water availability is not necessarily a yield limiting factor, yield gaps could be even larger, suggesting that additional fertilizer rates such as ca. 200 kg N ha⁻¹ could further dramatically increase yields. However, given that the yield-scaled N₂O emission in the MF treatment is more than twice as high as the average yield-scaled N₂O emission of 0.21 kg N₂O-N ton⁻¹ for maize globally and more than four times higher than the average yield-scale N₂O

emission of 0.12 kg N₂O-N ton⁻¹ for maize in Africa specifically³², our study illustrates that closing maize yield gaps in the Congo Basin with mineral fertilizers will come at the cost of particularly high N₂O emissions. This discrepancy likely arises from the distinct climatic conditions of the Congo Basin compared to those in the broader continental dataset. The meta-analysis by Yao et al.³² is heavily weighted toward studies from semi-arid and savanna regions of Africa (Kenya, Zimbabwe, Tanzania, Ethiopia), where soil moisture is low, limiting microbial denitrification. In contrast, the high rainfall and humidity of the Congo Basin maintain high water-filled pore space (WFPS), promoting anaerobic conditions that favor rapid denitrification. Consequently, nitrogen fertilization in this humid equatorial setting induces significantly higher N₂O loss per unit of yield.

Soil moisture conditions regulate N₂O emissions in these systems. Compared to the first maize trial, N₂O emissions were more pronounced in the wetter second trial, with also fertilizer N₂O peaks being significantly higher. This was controlled by high soil moisture following N application,

Optimizing Yield-Scaled N₂O Emissions

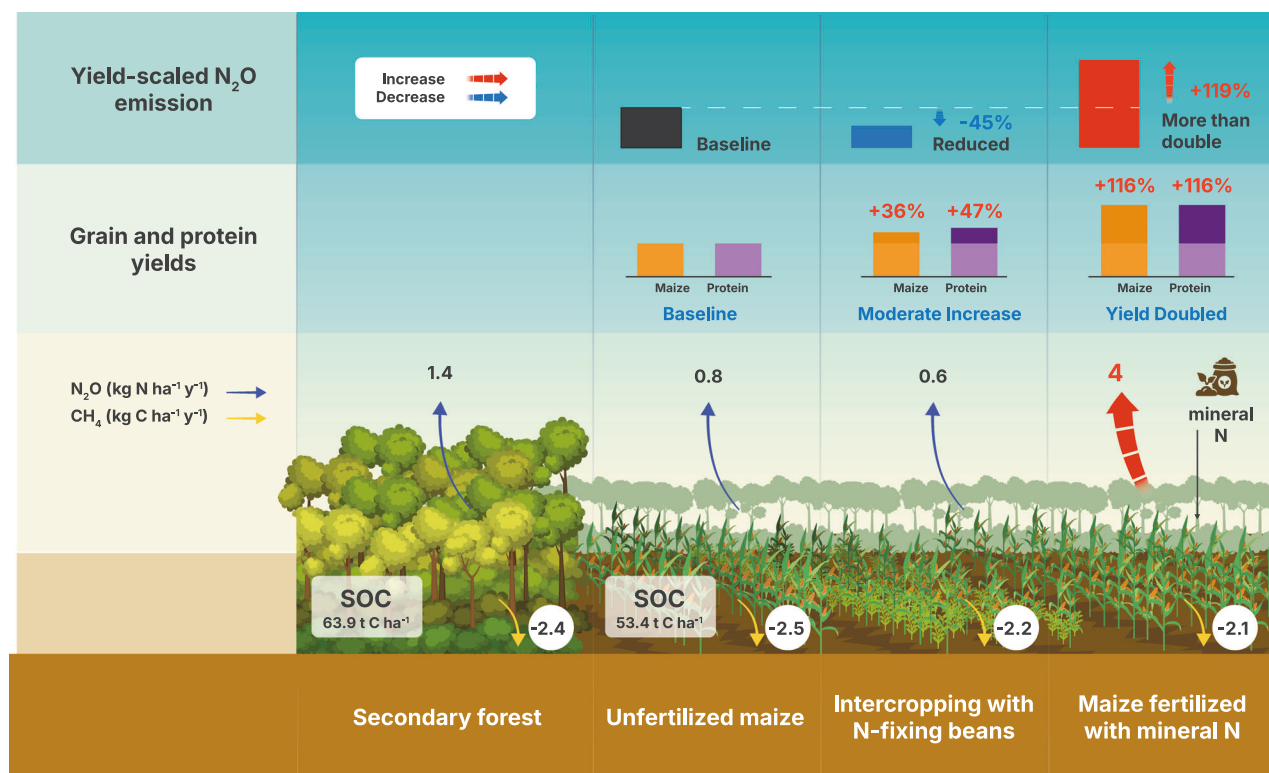


Fig. 6 | Effects of maize intensification on yield-scaled N₂O emissions, maize grain and protein yields, and greenhouse gas fluxes in the Congo Basin. The illustration compares four land-use systems: secondary forest, unfertilized maize, maize intercropped with N-fixing beans, and maize fertilized with mineral N,

highlighting changes in soil organic carbon (SOC) stocks, N₂O emissions, and maize and protein yields. Created in BioRender. Kwatcho Kengdo, S. (2026) <https://BioRender.com/8j976ci>.

which was 0.21 m³ m⁻³ in the first maize trial (average of 3 days following fertilization) versus 0.31 m³ m⁻³ in the second. Soil moisture, through its regulation of anaerobic soil volume and consequently of denitrification^{61,62}, was a dominant driver not only for N₂O but also for CH₄ and CO₂ fluxes, as observed in all three maize treatments and the SF. This observation aligns with previous findings in an adjacent unfertilized mixed crop field and an agroforest²⁹.

Both during the less wet first season and the more wet second season, the forest exhibited higher N₂O emissions than the MB and MC treatments but lower emission than the MF treatment (Fig. 3). Thus, mineral fertilizers persistently elevated N₂O emissions to levels well above those of natural ecosystems (Fig. 6). This is remarkable given that high N inputs via biological N fixation as well as high soil moisture and microbial activity in tropical forests lead to already high N₂O background emissions⁶². These natural N₂O emissions have been reported to strongly decrease after conversion to agroforests and mixed crop fields in the Congo Basin in the absence of mineral fertilizers²⁷. However, the very strong response of N₂O emissions to mineral fertilizer in this study highlights that the potential for high N₂O emissions is not generally lost after conversion of forests to crop fields. Instead, N₂O emissions can further increase global warming potential of forest conversion to fertilized crop fields on top of CO₂ emissions from SOC loss. In our study, these SOC losses amounted to 10.5 t C ha⁻¹ at a depth of 0–30 cm in 5 years due to the conversion of forest to cropland (Table 2 and Fig. 6). The cumulative N₂O emissions observed in the MF treatment were more than three times higher than the mean global average of 1.2 kg N ha⁻¹ yr⁻¹ in tropical rainforest ecosystems⁶³. Since the global warming potential of 3 kg additional N₂O-N emissions ha⁻¹ yr⁻¹ is equivalent to a SOC loss of 350 kg C ha⁻¹ yr⁻¹, these additional N₂O

emissions cannot be neglected when assessing GHG emissions from land-use change in the Congo Basin.

The SF and all three maize systems acted as overall net sinks of CH₄, with a more pronounced uptake in the MC treatment followed by the SF. Quantitatively, the net CH₄ sink was of minor importance for the overall GHG balance of the SF to maize conversion and the maize intensification. The net CH₄ uptake can be attributed to the dominant methanotrophic activity. Its persistence, except for a few measurement dates under very wet soil conditions is somewhat surprising given the high precipitation and high soil respiration rates, factors hampering gas diffusion but increasing O₂ consumption in the soil air. This persistent net CH₄ uptake may be related to the high sand content (Table 2), which resulted in well-aerated soils, allowing for sufficient gas diffusion in soil for continuous net CH₄ oxidation. The low CH₄ emissions observed in the second maize trials highlight the role of higher soil moisture in promoting conditions favorable for soil methanogenesis in soil⁶⁴. The cumulative CH₄ uptake in this study is within the range of values observed in tropical ecosystems worldwide⁶⁵. However, CH₄ uptake in the three maize systems was slightly higher than in an adjacent unfertilized mixed crop field²⁹. We also found that the maize + mineral N treatment had the lowest CH₄ uptake compared to the other maize treatments and the SF. This finding may indicate that mineral N application may reduce the capacity for CH₄ oxidation, possibly due to the inhibition of methanotrophic bacteria in the soil due to the homology of the enzymes for ammonia oxidation and CH₄ oxidation^{66,67}.

With the projected increase in human population in the Congo Basin, there is an urgent need to address key dual sustainable development goals: increasing food production while mitigating climate change. This pioneering case study on trade-offs between yield increases and GHG emissions

provides clear pointers for sustainable intensification of maize cultivation, which need to be supplemented by further work in the vast Congo Basin area. Our findings suggest that maize intensification based on mineral N fertilization strongly increases grain yields but at the cost of very high N_2O emissions, and also slightly reduced the CH_4 sink strength. In contrast, maize intercropping with N-fixing beans could offer a promising approach for sustainable maize intensification in the Congo Basin, but it is far from being able to close the yield gap in the short-term. Still, this approach saved costs for mineral fertilizers, even tended to reduce N_2O emissions compared to an unfertilized maize control, and left the soil CH_4 sink capacity unchanged, while providing additional protein-rich food as a co-benefit (Fig. 6). This approach is therefore appropriate and recommended for regions with limited access to mineral fertilizers, where protein malnutrition and food security are pressing issues and where soils are prone to high N_2O emissions due to wet conditions.

Methods

Study site and site description

The study was carried out in the Ayos district located in the Centre region of Cameroon. The site has a subequatorial climate with a bimodal rainfall regime. The long dry season occurs between December and March, and the short, between July and August. Rainy seasons occur from April to June and September to November. Mean annual temperature and precipitation were 27 °C and 1700 mm, respectively (Fig. 3A). Experiments were conducted in a 20-year-old secondary forest (SF) (705 m a.s.l.; 3°58'21.1"N; 12°25'17.5"E) and three maize crop fields (725 a.s.l.; 3°58'01.3"N; 12°26'34.5"E). *Irvingia sp.*, *Strombosia grandifolia*, *Musanga cercropiodes* and *Terminalia superba* mainly dominated the vegetation in the SF. Soils were characterized as Ferralitic red soils (Oxisols)⁶⁸ or Acric Ferralsols⁶⁹.

Experimental design

The experiment was conducted over two consecutive growing seasons in 2015. Just before the beginning of the first rainy season, we established three adjacent experimental maize fields, each measuring 0.1 ha (20 × 50 m²), on land that local farmers had recently cleared (<5 years). The three treatments included an unfertilized maize control (MC), maize intercropped with N-fixing beans (MB), and maize fertilized with mineral N (MF). For all fields, the vegetation was cleared by hand using machetes and subsequently burned following common local practices. The soil was then ploughed manually with hoes, and maize seeds (CMS 8501 variety, approved by the Cameroonian Institute of Agricultural Research for Development, IRAD) were sown by hand at a depth of 4–5 cm with three seeds per planting hole. A planting density of 75 × 50 cm² (inter-row × intra-row spacing) was maintained. Sowing for the first season took place on May 1, and for the second season on September 5. In the MB treatment, beans were introduced in an additive, within-row pattern, with two bean seeds sown at the mid-point of each 50 cm intra-row maize interval.

After germination, maize plant density was adjusted to ca. five plants per m⁻² by carefully removing one plant, leaving two maize plants per hole for the duration of the experiment. In the MB treatment, common beans (*Phaseolus vulgaris* cv. ECA PAN 021) were intercropped with maize at the same spacing. The MF treatment received nitrogen in split doses. In the first season, an initial application of 50 kg NPK mixture ha⁻¹ (20-10-10%) and 25 kg urea ha⁻¹ (46% N) was performed on May 11 (2 weeks after sowing), followed by a top-dressing of 25 kg urea ha⁻¹ on June 25 (after the appearance of the male maize flowers). Similarly, in the second season, the initial fertilizer application occurred on September 22, with the top-dressing applied on November 4. This equaled a total addition of 33 kg N ha⁻¹ for each growing season and 66 kg N ha⁻¹ for the entire experiment. Weeding was performed manually twice per season. The first maize crop was harvested on August 26 and the second on December 29, resulting in a growing cycle of approximately 4 months per season. This annual double-cropping system (Fig. 1) follows standard local agricultural practices in the Ayos district, which experiences a bimodal rainfall regime. The SF control was

located approximately 3 km from the maize field and had the same topography, bedrock geology, and climate.

At physiological maturity, biomass sampling was conducted over a total area of 150 m² per treatment, subdivided into six 25 m² sampling plots each. Within each sampling plot, the total number of plants and cobs was counted. For detailed yield and biomass estimation, five representative maize plants were randomly selected from each 25 m² plot and uprooted. The plants were partitioned into stems, roots, and cobs, and fresh weights were recorded immediately. Sub-samples were then oven-dried at 65 °C for 48 h to determine dry matter content. After drying, grains were separated from the cobs and weighed. Grain yield per hectare was estimated by multiplying the average dry grain weight per plant (from the 30 sampled plants) by the plant population per hectare (calculated from the counts in the 150 m² area).

Soil chemical characterization

Soil pH, calcium (Ca), magnesium (Mg), potassium (K), and phosphorus (P) concentrations were determined from soil samples collected at a depth of 0–20 cm in each treatment in December 2015 (with 12 replicates in the secondary forest and 6 replicates in each maize treatment). Samples were air-dried and sieved through a 2 mm sieve. Soil pH was measured in water and 1 N KCl solutions using a combination electrode in a 1:2.5 (w/v) soil-to-water suspension⁷⁰. Soil texture (in the unfertilized maize control and SF), total nitrogen (N), and organic carbon (C) content (%) at 0–10 and 10–30 cm depths were determined from undisturbed soil cores collected from a single pit per treatment (vertical sampling of using steel cores). Bulk density was determined on oven-dried subsamples at 105 °C. Cation exchange capacity (CEC) was measured using the ammonium acetate method at pH 7⁷¹. Finely ground and sieved (0.5 mm) subsamples were analyzed for total N and organic C%. Organic C was determined by chromic acid digestion⁷², and total N was measured using a two-step digestion with hydrogen peroxide and sulfuric acid⁷³.

Mineral N concentrations

Soil samples were collected at least weekly during each growing season, with an increased frequency following mineral N application in the MF. On each occasion, three soil samples were randomly taken from each maize field at a depth of 0–5 cm. A pooled sample was extracted with 1 M KCl at a soil-to-solution ratio of 1:4⁷⁴. Ammonium (NH_4^+) and nitrate (NO_3^-) concentrations were determined using the sodium salicylate reaction⁷⁵ and the Griess-Illorvay reaction⁷⁶, respectively. Concentrations were expressed on a dry mass basis (using gravimetric water content) and converted to stocks using bulk density measurements determined from the soil pits. The concentrations of minerals N and C were transformed into stocks by multiplying them with bulk density and the relevant soil depth.

Soil-atmosphere exchange of greenhouse gases

Soil gas samples were collected at weekly intervals for all treatments during both maize growing seasons using a manual static chamber method. The sampling frequency was increased to three times per week for the 2 weeks following each fertilizer application to better capture potential N_2O emission pulses. All gas sampling was standardized to the midday period (11:00 AM–3:00 PM local time) to minimize bias due to diurnal variation. Manual sampling of chambers with syringes was conducted according to Arias-Navarro et al.⁷⁷. Permanent frames (or collars; 26.7 × 37.3 × 11.5 cm) were inserted 5 cm into the soil at the beginning of the experiment. In the MC treatment, six frames were established, and seven for each of the MB and MF treatments. During each gas sampling event, an airtight chamber (equipped with a fan and vent) was sealed onto each frame. The identical flux measurement approach was used in the SF, as described by Verchot et al.²⁹. For each flux measurement, five gas samples were collected from each chamber headspace (equipped with a fan) at 0, 5, 10, 15, and 25 min using a 60 mL syringe. Gas samples were transferred into 10 mL vials, with the first 40 mL used to flush the headspace and the remaining 20 mL injected into the vial to

create overpressure. Soil temperature and moisture at 5 cm depth were measured near each chamber using a Procheck handheld reader coupled to a GS3 sensor (Decagon Devices, Inc., USA). The temperature within the chamber was measured at the beginning and end of each flux measurement using a handheld thermometer.

Gas samples were analyzed within a week using a gas chromatograph (SRI 8610C, SRI Inc., USA) at the gas chromatography facilities of the Center for International Forestry Research (CIFOR) located at the Institute for Tropical Agriculture (IITA) laboratory in Yaoundé, Cameroon²⁹. A flame ionization detector (FID) and a methanizer were used to detect CO₂ and CH₄, while a ⁶³Ni electron capture detector (ECD) was used to detect N₂O. Gas fluxes were calculated from the linear changes in gas concentration in the chamber headspace over the five time points using the ideal gas law. The total cumulative flux over the two maize trials was calculated using the linear interpolation method. For this, daily fluxes were calculated from the measurements, and gap filling for other days was based on the assumption of linear changes between measurement points. N₂O emissions were weighted as a function of maize grain yield (i.e., N₂O emissions per unit of maize grain yield: referred to as yield-scaled N₂O emissions) by dividing N₂O emissions (in kg N ha⁻¹ yr⁻¹) by maize grain yields (in kg ha⁻¹)^{58,78}. N₂O and CH₄ fluxes were converted into CO₂-eq using their global warming potential (273 and 27.2, respectively) over 100 years³³. Protein yield was estimated using an average protein content of 9.4% and 22.1% for white maize grain and common beans, respectively, as reported by the FAO food composition database⁷⁹.

Statistical analysis

All statistical analyses and visualizations were performed using R software⁸⁰. Data normality was assessed using the Shapiro-Wilk test prior to analysis. T-tests were conducted to compare plant biomass between the two maize trials. Analysis of variance (ANOVA) was used to determine differences in maize grain yield and soil chemical properties among land-use types. Spearman correlation analysis examined the relationships between CO₂, N₂O, and CH₄ fluxes and soil moisture and temperature within each maize field. A linear mixed-effects model was used to evaluate the impact of land use type (SF, MC, MB, MF) on GHG fluxes using the *lme4* package. Land use type was treated as a fixed factor, while sampling dates were included as a random effect. Post-hoc comparisons were conducted using the *emmeans* package. Statistical significance was set at $\alpha = 0.05$ for all tests.

Data availability

The data supporting the findings of this study are available in the Dryad repository: <https://doi.org/10.5061/dryad.flvhhmb5>.

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Author contributions

M.D., L.V.V., M.C.R., D.J.S., and K.B. designed the study. S.K.K., L.D.D., C.B.N., J.T., and D.J.S. performed experiments and data analysis. S.K.K., C.B.N., D.J.S., and M.D. wrote the manuscript with input from all the authors. Mariana C. Rufino passed away on September 14, 2025, shortly before the submission of this paper. She conceptionally contributed to the study design, and revised earlier and the pre-final version of this manuscript. Her contribution to this research was invaluable, and she will be deeply missed. All authors have read and approved the manuscript.

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Competing interests

The authors declare no competing interests.

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