



Interaction between water, crop residue and fertilization management on the source-differentiated nitrogen uptake by rice

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Abstract

Alternate wetting and drying (AWD) is an effective water-saving practice for rice cultivation that may however promote nitrogen (N) losses compared to continuous flooding (CF). The interaction between water, crop residue and N fertilization management can influence the contribution of different N sources to plant uptake. We hypothesized that microbial processes driving the source-differentiated N supply for rice uptake during the early growth stages will depend on the interaction between water management, the timing of straw incorporation with respect to flooding and the temporal distribution of mineral N application. Rice was grown for 60 days in mesocosm experiment involving a factorial design with (i) two water regimes (CF vs. AWD) and (ii) three straw and fertilizer managements, during which soil N, porewater chemistry, plant growth and N uptake were evaluated. Source partitioning of plant N between fertilizer-, straw- and soil-derived N was achieved by means of a dual-stable isotope ¹⁵N tracing approach. Although AWD reduced total N uptake by about 4–25% with respect to CF, this could only be partly attributed to a lower uptake of fertilizer-N (and lower fertilizer-N use efficiency), suggesting that other N sources were affected by water management. Our findings evidence how the interaction between soil redox conditions and the availability of labile C and inorganic N strongly determined the supply of soil-derived N through microbial feedback and priming responses. Although incorporated straw contributed only minimally to rice N, it represented the primary driver controlling plant N nutrition through these microbial responses. These insights may contribute to identify suitable fertilization practices that favour plant N uptake during the early stages of rice growth under AWD.

Keywords Alternate wetting and drying · Rice straw management · N fertilization · ¹⁵N isotope source partitioning · N rice uptake · Fertilizer use efficiency

Introduction

Rice cultivation with conventional continuous flooding (CF) requires large amounts of water, with the production of 1 ton of rice grain requiring approximately 2500 tons of water (Bouman et al. 2009). Moreover, water for agriculture is becoming increasingly scarce, due to climate change-related variations in rainfall patterns, decreasing resources and quality, inefficient irrigation systems and competition from other

sectors such as urban and industrial users (Bouman et al. 2007). Adequate availability of water resources to sustain crop yields is thus one of the most pressing challenges rice cropping systems are currently facing (Arcieri and Ghinassi 2020).

In recent decades, the alternate wetting and drying (AWD) technique, in which fields are drained and re-flooded one or more times during the growing season, has become one of the most widespread water-saving irrigation technologies in paddy field (Song et al. 2020). AWD saves irrigation water by up to 38% (Shao et al. 2015; Carrijo et al. 2017; Song et al. 2021) and contributes to the reduction of CH₄ emissions, lowering the global warming potential with respect to CF (Li et al. 2018; Malumpong et al. 2021), while maintaining or even improving yields (Lampayan et al. 2015; Lahue et al. 2016).

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However, the change of water management from CF to AWD may influence soil nutrient cycling and the functioning of soil microorganisms (Cao et al. 2022). Indeed, Yang et al. (1999) pointed out that drying and re-wetting cycles in AWD affect biochemical and physical processes, namely, nitrification, denitrification, mineralization, percolation and leaching in soil by changing soil water and air equilibrium, which in turn affects N availability for plant uptake. The effects of AWD on the N dynamics in the soil–plant system and on N use efficiency (NUE) have been widely investigated but giving contradictory findings. Several studies have reported that the alternation between aerobic and anaerobic soil conditions in AWD may promote nitrification and denitrification responsible for enhanced production of N_2O (nitrification and partial denitrification) or N_2 (total denitrification), as well as NO_3^- leaching and NH_3 volatilization, resulting in substantial N losses, lower plant N uptake and consequently a lower NUE (Tan et al. 2015; Miniotti et al. 2016; Dong et al. 2018; Li et al. 2018; Jin et al. 2020; López-Aizpún et al. 2021; Cheng et al. 2022). On the contrary, some studies demonstrated that there was no increase in N losses or even an enhancement of NUE with the adoption of AWD (Liu et al. 2013; Yang 2015; Wang et al. 2016; Djaman et al. 2018; Hameed et al. 2019; Islam et al. 2022). In addition, an improved soil aeration with AWD can accelerate organic matter mineralization enhancing the net release of available N for plant uptake from both soil organic matter (SOM) and incorporated crop residues (Zhang et al. 2009; Dong et al. 2012; Cucu et al. 2014; Chu et al. 2015; Fang et al. 2018). Thus, there is an increasing need to study the effects of AWD on NUE to optimize fertilizer-N management and reduce negative environmental impacts (Cheng et al. 2022; Wang et al. 2022).

The studies on the influence of water management on N availability for rice growth have always been confounded by the different effects that water management can have on the fate of applied N fertilizers and crop residue-derived N as well as native sources of soil organic N that are all known to contribute to plant nutrition (Said-Pullicino et al. 2014; Akter et al. 2018). Several studies have focused on evaluating the contribution of different N sources to rice nutrition under both CF and AWD conditions (Pan et al. 2012; Chen et al. 2016; Zhou et al. 2020); however, knowledge about the relative contribution of all three sources of N (fertilizer, crop residues and soil) as a function of water management is still poorly understood.

Crop residues and N fertilization management that are highly accountable for rice nutrition and for driving N availability in paddy soils are strongly coupled to water management practices (Bird et al. 2003; Kögel-Knabner et al. 2010; Said-Pullicino et al. 2014). It is well-known that poor N fertilizer use efficiency (30–40% recovery of applied N) occurs in continuously flooded rice systems (Cassman et al. 2002),

with the remainder of total N uptake by rice derived from native soil N (Reddy 1982; Cassman et al. 1998). Under periodic flooding and drying conditions, SOM and its redox properties play a crucial role in driving microbial processes that influence N availability for plant uptake and N losses (Nie et al. 2023). The release of N for plant uptake during straw decomposition depends on the balance between microbial N mineralization and immobilization, in turn affected by the availability of labile C sources for microbial activity and soil redox conditions (Nannipieri and Paul 2009). Moreover, both crop residue and water management practices adopted in rice cropping systems may strongly influence microbial and abiotic immobilization of applied fertilizer-N and consequently N availability for rice. In particular, lower soil redox conditions and the addition of labile organic matter may enhance N immobilization (27–50% of applied fertilizer-N under flooded conditions) (Devêvre and Horwáth 2000; Said-Pullicino et al. 2014) that may be subsequently released in time, contributing to available N for plant uptake (Devêvre and Horwáth 2001; Nannipieri and Paul 2009). Besides immobilization, the combination of crop residue and flood water management practices may strongly affect N losses from paddy fields representing between 10 and 65% of applied fertilizer-N (Cassman et al. 1998; Ghosh and Bhat 1998). Therefore, temporal synchrony between fertilizer, crop residue and indigenous N supply and plant uptake is a crucial factor in determining N use efficiency (Cucu et al. 2014).

This work aims to provide insights into how AWD affects N cycling in paddy soils and the contribution of different N sources to plant nutrition, with respect to CF practices, as a function of crop residue incorporation and mineral N fertilization. Although various studies have focused on the interactions between water, fertilizer and crop residue management on the availability and plant uptake of N in rice paddies, this study evaluates the effects of the interactions between water management and the timing of crop residue and fertilizer application on soil processes driving the partitioning between different N sources in their contribution to total plant N uptake. These insights are important in order to identify suitable fertilization practices that favour plant N uptake and minimize N losses particularly during the early stages of rice growth under AWD when most N losses in the field are recorded (Miniotti et al. 2016). We hypothesized that (1) AWD will decrease the contribution of fertilizer-derived N to plant N due to increased N losses but increase N derived from crop residue and SOM mineralization due to the faster degradation under oxic soil conditions; (2) anticipating the incorporation of rice straw with respect to soil flooding can promote their mineralization (and release of straw-N for plant uptake) under aerobic soil conditions and limit the immobilization of fertilizer-N during the growth period; and (3) increasing the amount of fertilizer-N applied

at seeding and reducing the amount applied at tillering (with the start of AWD cycles) can improve N supply by temporarily enhancing N immobilization by the microbial biomass and limiting the losses of fertilizer-N during redox cycling and stimulate the metabolic degradation of organic matter and release of soil- and straw-derived N (i.e. priming). We tested these hypotheses by a mesocosm experiment in which rice was grown for 60 days (vegetative stage) in a growth chamber, under two different water regimes (CF vs. AWD). The paddy soil received both mineral and organic N (in the form of rice straw). Changes in plant-available N and microbial biomass, plant development and N uptake during the growth period were followed. We adopted a dual-stable isotope ^{15}N tracing approach to partition plant N between fertilizer-derived, straw-derived or indigenous N, in order to identify those sources and processes that have a major influence on N availability and plant nutrition.

Materials and methods

Soil and straw properties and mesocosm design

Soil was collected from the Ap horizon (0–15 cm) of a paddy soil (Haplic Gleysol) located within the Rice Research Centre of Ente Nazionale Risi at Castello d'Agogna (45°14'48"N, 8°41'52"E, NW Italy). The field has been under continuous rice cultivation for the last 30 years, with crop residue incorporation in spring, and field flooding for most of the cropping period (May to September). Soil was collected at the end of the cropping season (October) after removal of straw on the surface. The collected soil was air-dried and sieved at 5 mm. The main physicochemical properties of the soil are organic C, 11.8 g kg⁻¹; total N, 1.3 g kg⁻¹; pH, 5.9; CEC, 9.4 cmol kg⁻¹; exchangeable Ca²⁺, Mg²⁺ and K⁺, 38.5, 12.6 and 20 mg kg⁻¹, respectively; P Olsen, 20.1 mg kg⁻¹; clay, 101 g kg⁻¹; silt, 463 g kg⁻¹; and sand, 437 g kg⁻¹. Rice straw was obtained from a previous field experiment in the same experimental platform, in which rice plants were repeatedly labelled with isotopically enriched N fertilizer (urea, 2.000 atom% ^{15}N) to ensure uniform enrichment of the straw at harvest and that had an isotopic enrichment of 0.925 atom% ^{15}N . Non-enriched rice straw was sampled from the same field from plots that received natural abundance urea fertilizer. The total N contents of non-enriched and ^{15}N enriched straw were 6.1 g N kg⁻¹ and 5.7 g N kg⁻¹, respectively, while the total C contents were 372 g C kg⁻¹ and 362 g C kg⁻¹, respectively.

Mesocosms were built using a cylindrical polyvinyl chloride (PVC) pipe (75 mm inner diameter, 350 mm height), whose bottom was closed with a non-woven fabric to allow for changes in water potentials during flooding and drainage periods (Fig. 1). Each mesocosm was filled with 1 kg

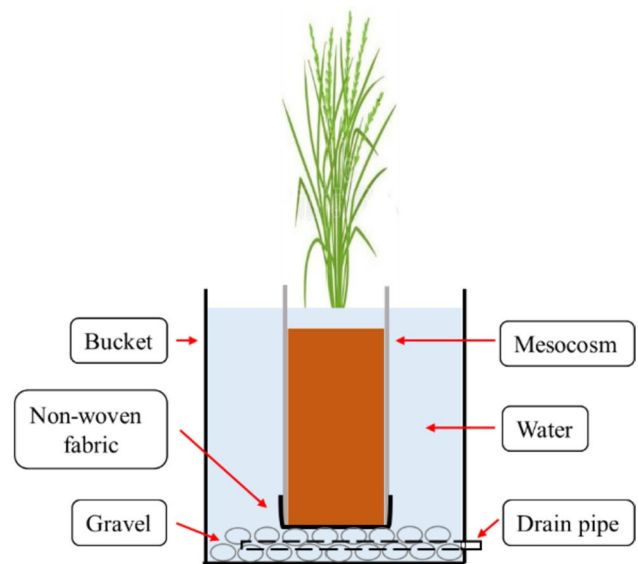


Fig. 1 Representation of mesocosm and system adopted for water management in the experiment

of soil (oven dry basis) and placed inside a bucket (300 mm diameter, 400 mm height) containing 5 cm of gravel at the bottom on which the mesocosms rested, in order to allow water management during flooding and drainage periods. Changes in soil water potential inside the mesocosms during the experiment were controlled by regulating the water level in the buckets: flooding was carried out by introducing water into the bucket until the water level in the mesocosm and bucket were both around 3 cm above the soil level, while drainage was managed by reducing the water level in the bucket to the desired level through a plastic drain pipe. The mesocosms were located inside a growth chamber during the whole experimental period.

Experimental design

The experimental design comprised a completely randomized 2 × 3 factorial arrangement with water management as the main factor (continuous flooding (CF) vs alternate wetting and drying (AWD)) and three combinations of straw and fertilizer management as the second factor (Table 1). The three treatments differed in the timing of straw incorporation with respect to seeding (30 vs 60 days before seeding; S30 and S60, respectively) and in the splitting of applied fertilizer-N (52.8 mg N kg⁻¹ soil, equivalent to 120 kg N ha⁻¹, considering a mesocosm area of 44 cm²) between pre-seeding and tillering stage (60 + 60 vs 80 + 40 kg N ha⁻¹; N60-N60 and N80-N40, respectively). S30-N60-N60 is the conventionally applied treatment in the Italian rice cultivation system, while S60-N60-N60 and S30-N80-N40 allowed to test hypotheses 2 and 3, respectively.

Table 1 Details of the differences in water, straw and fertilization management between the different experimental treatments

Water management ^a	Treatment	Straw incubation (days before seeding)	N fertilization (kg N ha ⁻¹)	
			Pre-seeding	Tillering
CF	S30-N60-N60	30	60	60
	S30-N80-N40	30	80	40
	S60-N60-N60	60	60	60
AWD	S30-N60-N60	30	60	60
	S30-N80-N40	30	80	40
	S60-N60-N60	60	60	60

^aCF continuous flooding; AWD alternate wetting and drying

Each of the three treatments was replicated in 9 mesocosms, in order to obtain 27 mesocosms for each water management. To investigate the different contribution of fertilizer-, straw- and soil-derived N to plant nutrition, ¹⁵N-labelled materials were used in dedicated mesocosms. Three of the 9 replicated mesocosms for each treatment previously described received ¹⁵N-labelled straw and natural abundance fertilizer (15SN), and another three received natural abundance straw and ¹⁵N-labelled fertilizer (S15N), while the last three received natural abundance straw and natural abundance fertilizer (SN). Mesocosms were destructively sampled at 60 DAS for both CF and AWD, while an additional set of 27 mesocosms was specifically set up for sampling at 30 DAS, although these were managed only under CF since water management up to 30 DAS was the same for both CF and AWD (see water management details below).

Experimental conditions

Water management Soil moisture during straw incubation in the soil was maintained at 50% of field capacity (equivalent to a water content of 13% on a dry weight basis) gravimetrically. Just before flooding, pre-seeding fertilization was performed. Then all mesocosms were flooded, and water seeding was performed. Flooding was maintained for 30 days after seeding (DAS) by daily replacing the water lost by evapotranspiration. At 30 DAS (corresponding to tillering stage), the mesocosms were drained and fertilized. Half of the mesocosms (CF management) were re-flooded until the end of the experiment at 60 DAS. The other half were subjected to three 10-day AWD cycles each involving 4–5 days during which the water level in the bucket was gradually lowered to simulate the natural infiltration rates in the field, followed by 5 days of free drainage during which the soil was allowed to reach 73% water-filled pore space equivalent to a soil water potential of –20 kPa.

Straw management Natural abundance and ¹⁵N-enriched rice straw were chopped into 0.5-cm segments and added to the soil 30 or 60 days before seeding. A straw application dose of 4.4 and 4.7 g kg⁻¹ of soil d.w., equivalent to a field application dose of 10 Mg ha⁻¹ d.w., was used for non-enriched and ¹⁵N-enriched straw, respectively, in order to supply the same absolute amount of straw-derived N (26.7 mg N per mesocosm) due to small differences in their N contents.

Fertilizer management Mineral N was added to the mesocosms in the form of ammonium sulphate just before seeding and at tillering stage (30 DAS). Both ¹⁵N-enriched fertilizer (2 atom% ¹⁵N) and natural abundance were used. The fertilizer was added to each mesocosm in solution by dissolving an appropriate amount of salt in 50 ml of deionized water. In addition, all mesocosms received a basal fertilization of potassium and phosphorus before seeding in the form of monopotassium phosphate (KH₂PO₄) and potassium chloride (KCl) at a dose corresponding to 15 kg P ha⁻¹ and 50 kg K ha⁻¹.

Rice variety and growth conditions One plant of *Oryza sativa* L. variety CL26 was established in each mesocosm. The seeds were pre-germinated on cotton before transferring to the soil mesocosms. The plants were grown in a controlled-environment growth chamber, equipped with LED lamps (Valoya, mod. LEDBX120C2), with 12 h of light (700 μmol m⁻² s⁻¹) and 12 h of dark, at 20 °C.

Porewater analyses

Soil solution was collected by means of Rhizon samplers (Rhizon MOM 19.21.22, Rhizosphere, Wageningen, the Netherlands) installed vertically in proximity of the root system at a depth between 5 and 10 cm, with three replicates per treatments (only in SN mesocosms). Porewater sampling was performed approximately every 10 days from seeding (0, 12, 22, 36, 47, 57 DAS) and immediately analysed for reduced iron (Fe^{II}), ammonium (NH₄⁺), nitrate (NO₃⁻) and dissolved organic C (DOC) concentrations. Dissolved Fe^{II} was determined following the method described by Loepfert and Inskeep (1996) involving reaction with 1,10-phenanthroline under acid condition. Ammonium (NH₄⁺) concentrations were determined spectrophotometrically by a modified Berthelot method involving reaction with salicylate in the presence of alkaline sodium dichloroisocyanurate (Crooke and Simpson 1971). Nitrate (NO₃⁻) concentrations in porewater samples were determined following the method described by Mulvaney (1996) which consists of quantitatively reducing NO₃⁻ to NO₂⁻ by addition of VCl₃ in the presence of Griess reagents and heating at 40 °C for 3 h. Dissolved organic C (DOC) was determined in acidified

(pH=2) aliquots of soil porewater by Pt-catalysed, high-temperature combustion (850 °C) followed by infrared and electrochemical detection of CO₂ and NO, respectively (Vario TOC, Elementar, Hanau, Germany) in a CO₂-free modified air carrier gas.

Soil analyses

Soil samples were collected from each mesocosm by means of a 10-mm diameter sampling probe at 30 and 60 DAS along the whole depth of the mesocosm explored by roots. Samples were immediately analysed for moisture content, inorganic N (ammonium and nitrate) content and microbial biomass C (MBC) as follows. Inorganic N was extracted from fresh soil samples with ammonium-free (NH₄⁺ < 0.001%) 1 M KCl (soil:solution ratio 1:5). After shaking for 60 min at 80 rpm, samples were centrifuged at 800 × *g* for 10 min and the supernatant filtered through a membrane with a pore size of 2.5 μm (Whatman No. 42). Inorganic N in the extracts was determined spectrophotometrically as described above. Soil moisture content was also determined gravimetrically after drying an aliquot at 105 °C for 24 h, in order to express all concentrations on a dry soil weight basis.

The microbial biomass C (MBC) in the soil was determined by using the chloroform fumigation-direct extraction method (Murage and Voroney 2007; Makarov et al. 2015; Setia et al. 2012). Soils were divided in two aliquots (10 g), one of which (non-treated) was extracted with 40 ml of 0.05 M K₂SO₄, while the other (CHCl₃-treated samples) was extracted with 40 ml of 0.05 M K₂SO₄ and 1 ml of ethanol-free chloroform. All samples were shaken for 1 h at 80 rpm, allowed to settle for 1 h and the supernatants decanted into clean containers that were subsequently ultracentrifuged for 15 min at 13,500 × *g* to obtain particle-free salt extracts. The chloroform-treated supernatants were purged with N₂ for 30 min to remove any residual CHCl₃. Total C concentrations in the extracts of the fumigated and non-fumigated samples were determined by a Vario TOC analyser (VarioTOC, Elementar, Hanau, Germany) using a combustion temperature of 680 °C. MBC was calculated by dividing the difference in DOC between the fumigated and non-fumigated extracts by an extraction efficiency value of 0.45 (Jenkinson et al. 2004).

Plant analyses

After soil sampling, plants were harvested at 30 DAS and 60 DAS at tillering and panicle differentiation stages, respectively. Roots were carefully washed with deionized water and then separated from shoots. Roots and shoots were dried at +45 °C to determine the dry biomass. All vegetal materials were ground to a fine powder with an ultracentrifugal

mill (Retsch mod. ZM 200). Total N contents and stable ¹⁵N isotope composition of plant samples were determined with an automated elemental analyser continuous flow isotope ratio mass spectrometer (IRMS; Vario Isotope Select and IsoPrime100, Elementar, UK). Plant N uptake over the rice growth period was calculated as the product of shoot or root biomass and their N contents. The fraction of plant N derived from fertilizer (*f*_{FDN}) was calculated from ¹⁵N isotope values by applying the following expression:

$$f_{\text{FDN}} = \frac{(\text{at}\%^{15}\text{N}_{15\text{N-plant}} - \text{at}\%^{15}\text{N}_{14\text{N-plant}})}{(\text{at}\%^{15}\text{N}_{15\text{N-fertilizer}} - \text{at}\%^{15}\text{N}_{14\text{N-fertilizer}})}$$

where at%¹⁵N_{15N-plant} and at%¹⁵N_{14N-plant} are the isotope ratio of shoot or root samples obtained from plants receiving enriched or natural abundance N fertilizer (¹⁵N-fertilizer or ¹⁴N-fertilizer), respectively (i.e. S15N and SN series). Natural abundance of ¹⁴N fertilizer used was equal to 0.366 atom% ¹⁵N. Fertilizer-derived N (FDN) in the shoots and roots was subsequently calculated as the product of *f*_{FDN} and N content in the respective plant part (N shoot or N root) and expressed in mg N mesocosm⁻¹. The fraction of plant N derived from the straw (*f*_{StDN}) was calculated in a similar way by applying a mixing model:

$$f_{\text{StDN}} = \frac{(\text{at}\%^{15}\text{N}_{15\text{-plant}} - \text{at}\%^{15}\text{N}_{14\text{-plant}})}{(\text{at}\%^{15}\text{N}_{15\text{-straw}} - \text{at}\%^{15}\text{N}_{14\text{-straw}})}$$

where at%¹⁵N_{15N-plant} and at%¹⁵N_{14N-plant} are the isotope ratio of shoot or root samples obtained from plants receiving enriched or natural abundance N straw (¹⁵N-straw or ¹⁴N-straw), respectively (i.e. 15SN and SN series). Natural abundance of ¹⁴N straw used was equal to 0.368 atom% ¹⁵N. Straw-derived N (StDN) in the shoots and roots was subsequently calculated as the product of *f*_{StDN} and N content in the respective plant part (N shoot or N root) and expressed in mg N mesocosm⁻¹. Soil-derived N (SDN) was determined as the difference between total plant N and the sum of fertilizer and straw-derived N.

In order to obtain an agronomic index about the efficiency of fertilization under the different treatments and to better investigate the ability of plants to acquire fertilizer-N, the fertilizer-N use efficiency (FUE) was calculated as the ratio between FDN in total plant (obtained from the sum of FDN in shoot and FDN in root) and the amount of N applied with fertilizer. For the calculation of FUE at 30 DAS, only the amount of N applied in pre-seeding was considered.

Statistical analysis

Data from samples collected at 30 DAS and 60 DAS were treated separately because at 30 DAS, only the effects of straw and fertilization management were evaluated, while at

60 DAS, also the effects of water management were evaluated. Data collected at the end of the experiment (NH_4^+ and NO_3^- content in soil, MBC, N plant uptake, FDN, StDN, SDN, FUE) were tested by ANOVA. In particular, one-way ANOVA was applied for data at 30 DAS and two-way ANOVA for data at 60 DAS. The Shapiro–Wilk test and Levene’s test were conducted to check the assumptions of normality and homogeneity of variance. When one of the assumptions was violated, a logarithmic transformation of data was applied. Treatment averages were separated by means of Bonferroni post hoc test at $p < 0.05$. Porewater data was analysed by applying the linear mixed-effect model for repeated measures with the “lme” function from the “nlme” R package. Statistical analysis was performed using R software version 4.0.5.

Results

Porewater and soil analyses

Changes in the concentrations of Fe^{II} in porewaters (Fig. 2) perfectly reflected water management. As expected, the Fe^{II} concentrations in CF generally increased after flooding and decreased with drainage at 30 DAS but maintained relatively high throughout the entire growing period. A similar increase in porewater Fe^{II} concentrations was observed in the first 30 DAS in AWD; however, with the start of the wetting

and drying cycles after 30 DAS, soil oxidation resulted in a drop in porewater Fe^{II} concentrations. Anticipated straw incorporation (S60) resulted in significantly lower porewater Fe^{II} concentrations with respect to straw incorporation near seeding (S30) in the 30 days after flooding, while no influence of fertilizer management was observed.

Anaerobic conditions prevailing during the whole growth period in CF and in the first 30 DAS in AWD resulted in a general increase in DOC concentrations (Fig. 2) with time. In contrast, the drainage of mesocosms at tillering stage in both CF and AWD treatments and the consecutive wetting and drying between 30 and 60 DAS in AWD resulted in lower DOC concentrations. Both S30 treatments induced significantly higher concentrations DOC with respect to S60 during the first 30 DAS, while no effects of fertilizer-N management on DOC concentrations were observed.

Porewater NH_4^+ concentrations remained relatively low after the first N fertilization at sowing across all treatments and only showed a slight increasing trend over the first 30 days (Fig. 3), whereas exchangeable NH_4^+ contents were highest at 30 DAS (Table 2). During the early stages of plant development, available N was not significantly affected by the amount of fertilizer-N applied in pre-seeding as both S30-N60-N60 and S30-N80-N40 showed similar amounts of exchangeable NH_4^+ (Table 2). In contrast, anticipating the incorporation of crop residues (60 days before seeding in the S60-N60-N60) resulted in significantly lower available NH_4^+ contents with respect to the other treatments.

Fig. 2 Variations in the concentration of reduced iron (Fe^{II}) and DOC in porewaters with time for continuous flooding (CF) and alternate wetting and drying (AWD) water management. Treatments involve straw incorporation 30 or 60 days before seeding (S30 and S60, respectively) and the splitting of applied N fertilizer between pre-seeding and tillering stage (60+60 vs 80+40 kg N ha^{-1} ; N60-N60 and N80-N40, respectively). Error bars represent standard errors calculated on three replicates. The asterisk denotes a significant difference ($p < 0.05$) among treatments. Shaded areas represent the moments in which the mesocosms were water saturated

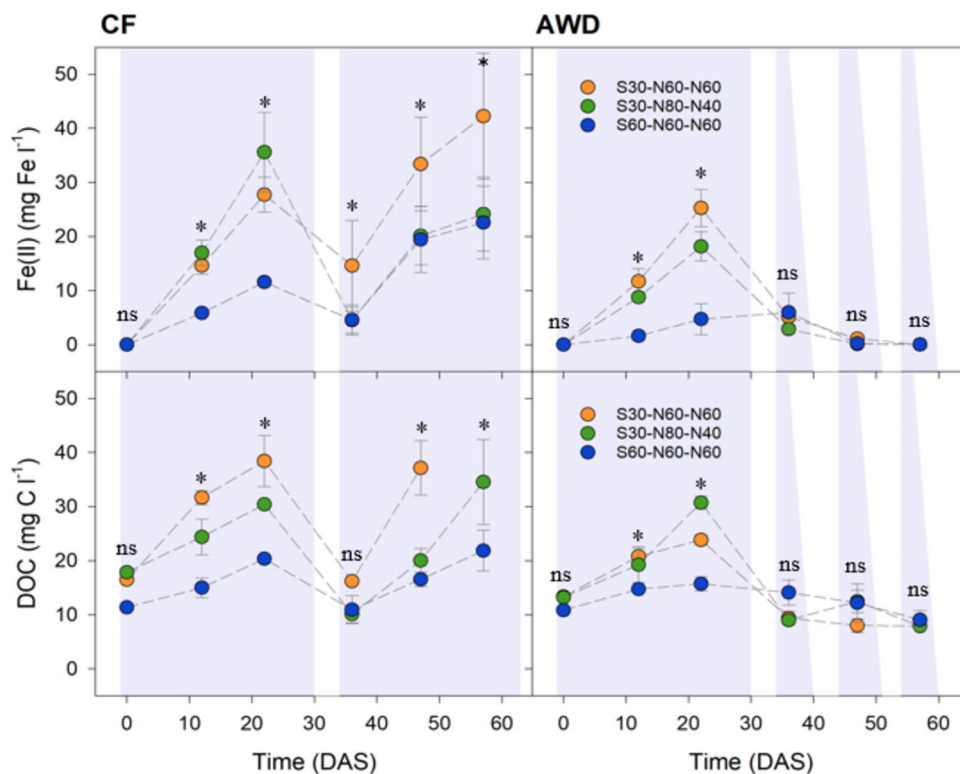


Fig. 3 Variations in the concentration of ammonium (NH₄⁺) and nitrate (NO₃⁻) in porewaters with time for continuous flooding (CF) and alternate wetting and drying (AWD) water management. Treatments involve straw incorporation 30 or 60 days before seeding (S30 and S60, respectively) and the splitting of applied N fertilizer between pre-seeding and tillering stage (60+60 vs 80+40 kg N ha⁻¹; N60-N60 and N80-N40, respectively). Error bars represent standard errors calculated on three replicates. The asterisk denotes a significant difference (*p* < 0.05) among treatments. Shaded areas represent the moments in which the mesocosms were water saturated, while dashed red lines represent fertilizer-N applications

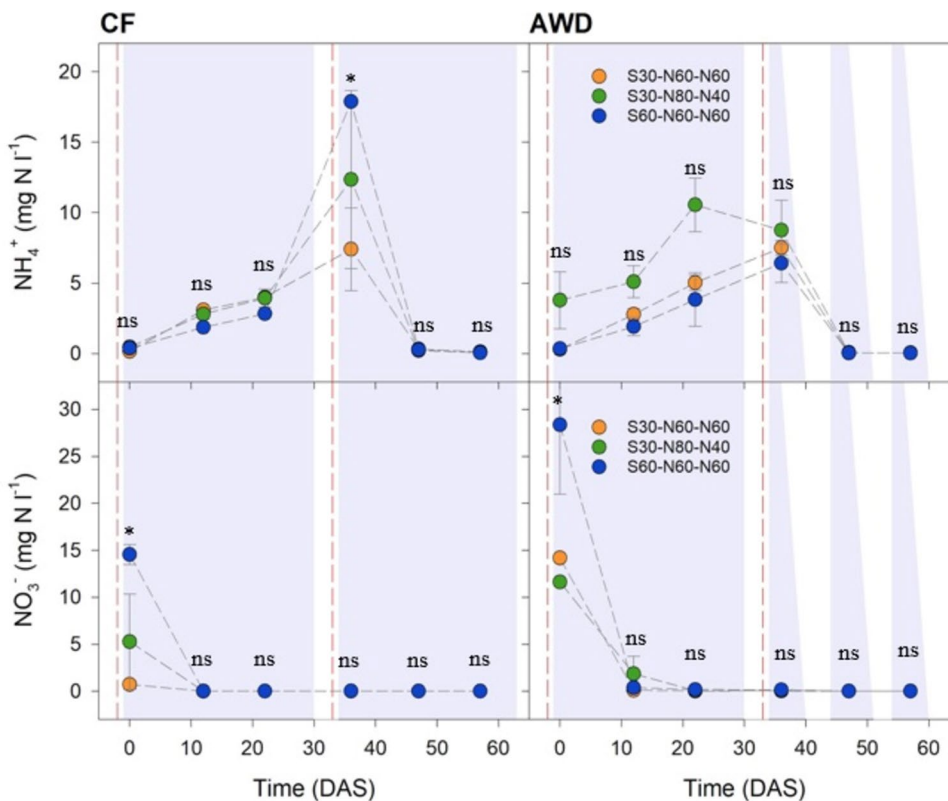


Table 2 Ammonium (NH₄⁺), nitrate (NO₃⁻) and microbial biomass C (MBC) in soil at different sampling times (30 and 60 DAS) in different water management (continuous flooding (CF); alternate wetting and drying (AWD)) and straw and fertilizer treatments (S30-N60-N60, S30-N80-N40, S60-N60-N60). Data are given as mean

values of the nine replicates ± standard deviation. Superscript lowercase letters indicate statistically significant differences between the treatments within water management (*p* < 0.05), while capital letters indicate statistically significant differences between water management (*p* < 0.05)

Sampling time	Water management	Treatment	NH ₄ ⁺ (mg N kg ⁻¹)	NO ₃ ⁻ (mg N kg ⁻¹)	MBC (mg C kg ⁻¹)
30 DAS	CF	S30-N60-N60	6.82 ± 2.34 ^a	0.16 ± 0.11	115.67 ± 107
		S30-N80-N40	6.31 ± 1.94 ^{ab}	0.10 ± 0.03	76.33 ± 29
		S60-N60-N60	4.22 ± 1.58 ^b	0.21 ± 0.23	117.5 ± 56
		Average	5.78	0.16	103.17
P (F) treatment			0.024	ns	ns
60 DAS	CF	S30-N60-N60	2.75 ± 1.77	0.19 ± 0.06	149.12 ± 172
		S30-N80-N40	2.44 ± 1.12	0.23 ± 0.08	105.2 ± 78
		S60-N60-N60	2.20 ± 0.88	0.23 ± 0.03	124 ± 146
		Average	2.46 A	0.22 B	126.11
	AWD	S30-N60-N60	0.45 ± 0.38	0.27 ± 0.04	136.88 ± 61
		S30-N80-N40	0.21 ± 0.23	0.34 ± 0.10	142.3 ± 41
		S60-N60-N60	0.25 ± 0.26	0.33 ± 0.06	109.67 ± 49
		Average	0.30 B	0.31 A	129.63
P(F) Water management			ns	0.020	ns
P(F) Treatment			0.000	0.000	ns
P(F) Water management * treatment			ns	ns	ns

Highest porewater NH_4^+ was observed immediately after fertilization at tillering stage (36 DAS), but porewater NH_4^+ concentrations subsequently decreased rapidly below detection limits in all treatments, probably due to the rapid plant N uptake and N losses. Similarly, exchangeable NH_4^+ contents in the soils were lower at 60 DAS than 30 DAS across all treatments, although contents were significantly lower under AWD with respect to CF (Table 2). A higher soil NO_3^- content under AWD than CF at 60 DAS was observed (Table 2). Nonetheless, porewater nitrate concentrations were generally below detection limits (Fig. 3), not only under the prevalent anoxic conditions when mesocosms were flooded (i.e. first 30 days in AWD and throughout the growth period in CF) but also during AWD cycles after tillering. High values were only recorded at seeding for the S60-N60-N60 treatment attributable to a greater degradation of early incubated rice straw, with a consequent net ammonium release and nitrification under oxidizing conditions.

Microbial biomass C in the soils did not show any significant differences between treatments irrespective of water, straw or fertilization management (Table 2).

Plant analyses

The adoption of AWD generally resulted in a lower plant development over the studied growth period, related to significantly lower leaf and especially root development,

resulting in a higher, although not significant, shoot-to-root ratio than CF (Table 3). As expected, a higher pre-seeding N fertilization in the S30-N80-N40 treatment determined a significantly higher shoot and root biomass at 30 DAS with respect to the other treatments that received 25% less fertilizer-N. This difference was still observed at 60 DAS only under CF whereby plants receiving a higher amount of mineral N in pre-seeding (i.e. S30-N80-N40 treatment) had significantly higher biomass than those receiving a more balanced splitting of the fertilizer-N between pre-seeding and tillering (i.e. S30-N60-N60 treatment; Table 3). Water management*treatment interaction showed that the incorporation of rice straw close to seeding in CF resulted in a significantly higher plant growth, compared to the early straw incorporation in CF, while under AWD, plant growth was similar across all treatments (Table 3).

AWD generally reduced total plant N uptake by about 4–25% in comparison to CF depending on the treatment (Fig. 4). Similar to what was observed for total plant biomass, a higher pre-seeding fertilizer-N dose led to a significantly higher plant N uptake at 30 DAS. On the other hand, in both CF and AWD, plant N uptake at 60 DAS was mainly influenced by the timing of straw addition with an early straw incorporation (S60) resulting in a significantly lower total plant N uptake with respect to a late incorporation (S30). Under CF irrigation, the best treatment for rice N nutrition appeared to be the S30-N80-N40, while in AWD,

Table 3 Shoot and root dry biomass and shoot-to-root ratio of plants at different sampling times (30 and 60 DAS) for the different water managements (continuous flooding (CF); alternate wetting and drying (AWD)) and straw and fertilizer treatments (S30-N60-N60, S30-N80-N40, S60-N60-N60). Data are given as mean values of the nine replicates \pm standard deviation. Superscript letters indicate

statistically significant differences between treatments at 30 DAS; superscript italic letters indicate statistically significant differences for water management * treatment interaction at 60 DAS ($p < 0.05$), while capital letters indicate statistically significant differences between water managements ($p < 0.05$)

Sampling time	Water management	Treatment	Shoot dry biomass (g mesocosm ⁻¹)	Root dry biomass (g mesocosm ⁻¹)	Shoot-to-root ratio
30 DAS	CF	S30-N60-N60	0.58 \pm 0.06 ^b	0.35 \pm 0.07 ^{ab}	1.67 \pm 0.28
		S30-N80-N40	0.76 \pm 0.15 ^a	0.43 \pm 0.09 ^a	1.77 \pm 0.23
		S60-N60-N60	0.56 \pm 0.07 ^b	0.32 \pm 0.05 ^b	1.80 \pm 0.39
		Average	0.63	0.37	1.75
P(F) treatment			0.004	0.006	ns
60 DAS	CF	S30-N60-N60	4.44 \pm 0.38 ^b	3.29 \pm 0.43 ^b	1.36 \pm 0.12
		S30-N80-N40	5.06 \pm 0.31 ^a	4.08 \pm 0.68 ^a	1.26 \pm 0.17
		S60-N60-N60	3.75 \pm 0.45 ^c	2.51 \pm 0.31 ^c	1.51 \pm 0.22
		Average	4.41 A	3.30 A	1.38
	AWD	S30-N60-N60	4.13 \pm 0.50 ^{bc}	2.66 \pm 0.43 ^c	1.57 \pm 0.15
		S30-N80-N40	3.66 \pm 0.47 ^c	2.22 \pm 0.47 ^c	1.72 \pm 0.41
		S60-N60-N60	3.56 \pm 0.45 ^c	2.12 \pm 0.21 ^c	1.68 \pm 0.19
		Average	3.78 B	2.33 B	1.66
P(F) Water management			0.000	0.000	ns
P(F) Treatment			0.000	0.000	0.000
P(F) Water management * treatment			0.000	0.000	ns

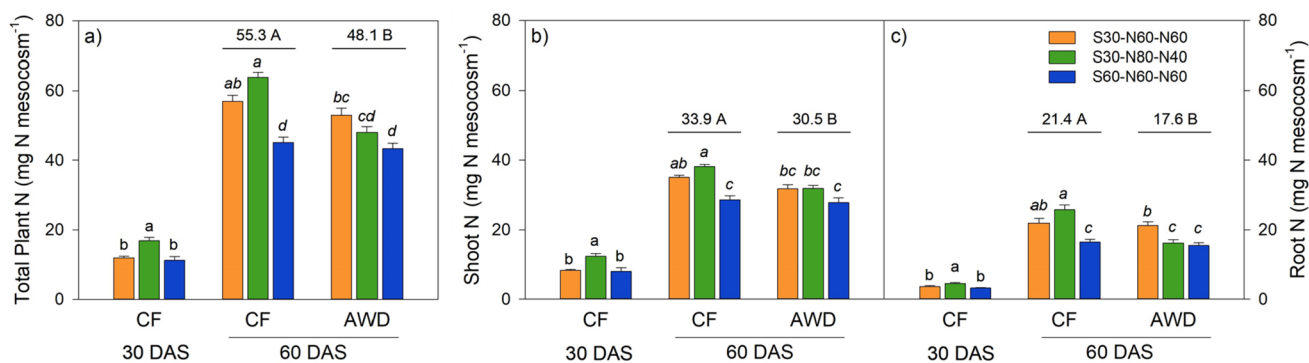


Fig. 4 Total plant N content (a) and contribution of shoot (b) and root (c) N to total plant N as a function of water management (continuous flooding (CF); alternate wetting and drying (AWD)) and straw and fertilizer treatments (S30-N60-N60, S30-N80-N40, S60-N60-N60). The numbers at the top show the average plant N for each water management at 60 DAS with capital letters indicating

statistically significant differences between averages ($p < 0.05$). Lowercase letters indicate statistically significant differences between the treatments at 30 DAS ($p < 0.05$), while lowercase italic letters indicate statistically significant difference for interaction water management*treatment at 60 DAS ($p < 0.05$)

the S30-N60-N60 showed the highest total plant N uptake at 60 DAS. The effects of water management and straw and fertilizer treatments on total shoot and root N mirrored what was observed for total plant N uptake suggesting no treatment effect on the distribution of plant N between different parts of the plant.

Figure 5 shows the relative contribution of fertilizer-, straw- and soil-derived N to rice N uptake in the shoots and roots as affected by water, straw and fertilizer management. This source partitioning of N allowed to observe that fertilizer-derived N (FDN) and soil-derived N (SDN) were the main contributors to total plant N, with straw-derived N generally contributing less than 5% of total plant N, across treatments. The contribution of FDN to both shoot and root N was significantly higher in CF than AWD (Fig. 5a, b), with early incorporation of rice straw (i.e. S60-N60-N60) leading to the highest amount of FDN especially in the shoot under both CF and AWD at 60 DAS. SDN, the other major contributor of N to the plant, was significantly higher in plants grown under CF than AWD (Fig. 5c, d). Treatments with straw incorporation 30 days before sowing (i.e. S30-N80-N40 and S30-N60-N60) showed a significantly higher contribution of SDN to plant uptake with respect to the treatment where straw was incorporated earlier (i.e. S60-N60-N60) under both CF and AWD water management. Water management did not affect the contribution of rice straw-derived N (StDN) to shoot N, although a significantly higher StDN in the roots was observed under CF with respect to AWD (Fig. 5e, f). A maximum percentage of 2.3% of shoot N and 3.4% of root N was derived from incorporated straw in the S30-N60-N60 treatment under CF at 60 DAS. As for SDN, rice straw management was the main driver of the main differences in StDN observed between the treatments. In fact, in most cases, the incorporation of rice

straw 30 days before seeding resulted in a greater contribution of StDN to plant N with respect to an early incorporation 60 days before seeding.

Considering the total amount of plant N derived from the applied fertilizer-N, CF showed a significantly higher mean fertilizer use efficiency (FUE) with respect to AWD at 60 DAS (Fig. 6). However, FUE under CF was not substantially influenced by the different straw and fertilizer treatments; the timing of straw incorporation strongly affected FUE under AWD. In fact, whereas a similar FUE was observed under both water managements when rice residues were incorporated 60 days before seeding, their late incorporation (in S30-N60-N60 and S30-N80-N40) resulted in significantly lower efficiencies under AWD.

Discussion

Influence of water management on N availability and plant uptake

With respect to CF, the adoption of AWD cycles after tillering was shown to result in a lower plant growth during the early vegetative stages, particularly for root development, in line with previous findings (Suriyagoda et al. 2014; Weerathne et al. 2015; Zhou et al. 2020; Wu et al. 2022). Several authors have however observed a positive plant growth response under AWD, with an increase in root length and dry matter accumulation (Kato and Okami 2010; Thakur et al. 2011; Hazra and Chandra 2016; Abid et al. 2022). It is well-known that rice plants grown under AWD can regulate the growth of above and belowground biomass in different proportions depending on the stage of the growing cycle (Zhang et al. 2021). Therefore, the lower root-to-shoot

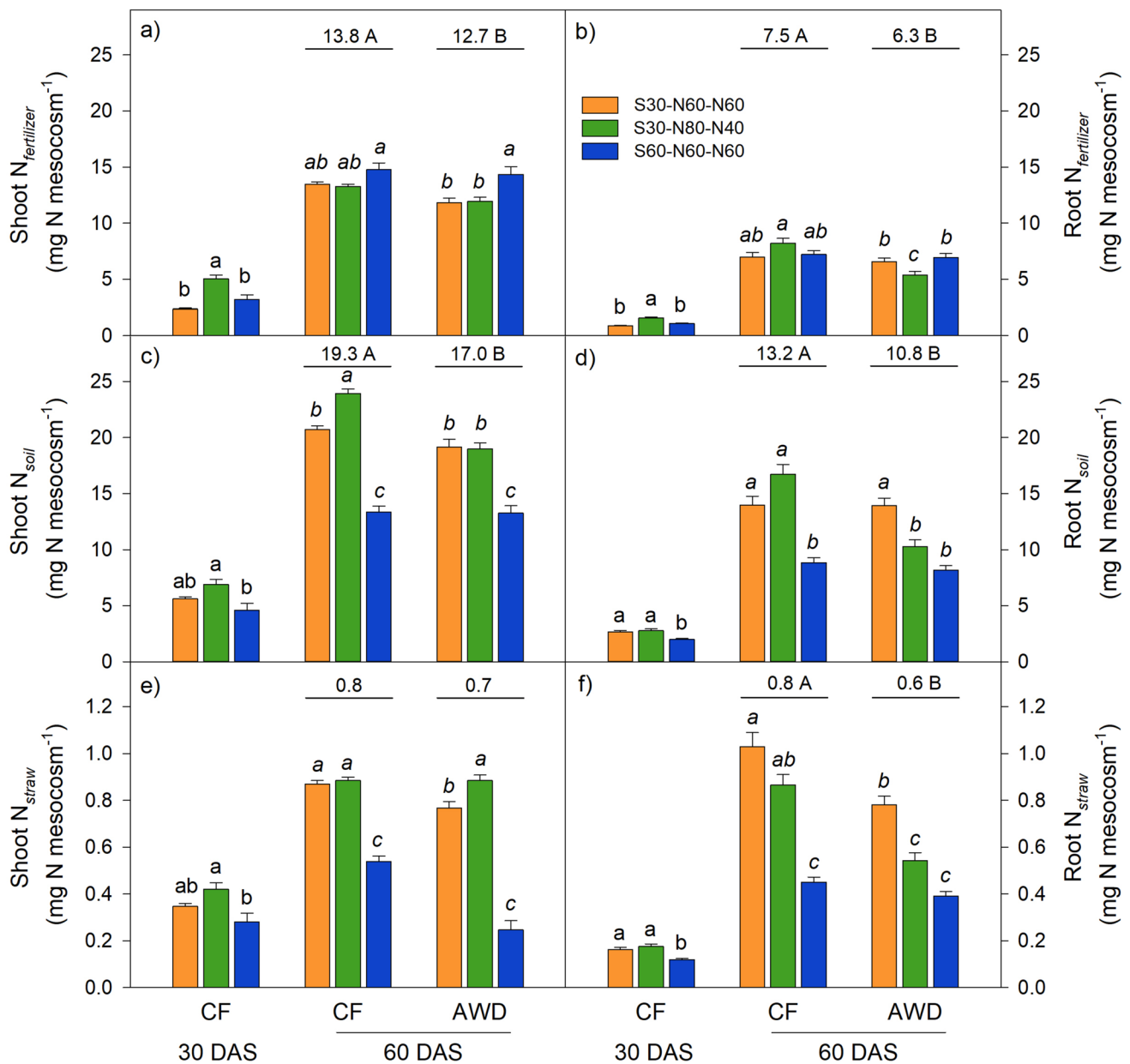


Fig. 5 Contribution of fertilizer (**a, b**), soil (**c, d**) and straw (**e, f**) to plant N uptake in the shoot (**a, c, e**) and root (**b, d, f**) as a function of water management (continuous flooding (CF); alternate wetting and drying (AWD)) and straw and fertilizer treatments (S30-N60-N60, S30-N80-N40, S60-N60-N60). The numbers at the top show the average shoot or root N for each water management at 60 DAS with

capital letters indicating statistically significant differences between averages ($p < 0.05$). Lowercase letters indicate statistically significant differences between the treatments at 30 DAS ($p < 0.05$), while lowercase italic letters indicate statistically significant difference for interaction water management*treatment at 60 DAS ($p < 0.05$)

ratio under AWD at panicle initiation stage observed in this experiment could be compensated at later phenological stages. This was already shown by Somaweera et al. (2016), among other studies, where the relationship between AWD and plant growth at field scale was investigated taking into consideration the entire crop cycle until harvest. Moreover, in our mesocosm experiment, the limited volume of soil and different environmental conditions may have differently

affected soil physicochemical properties and crop growth compared to field conditions (Jin et al. 2020).

The lower N uptake under AWD can be probably attributed to a lower root development, as previously observed by Barison and Uphoff (2011), as well as the well documented extensive N losses that occur during the consecutive redox cycles of AWD (Miniotti et al. 2016; Zhang et al. 2018). Indeed, it is reasonable to attribute the lower soil NH_4^+ availability observed

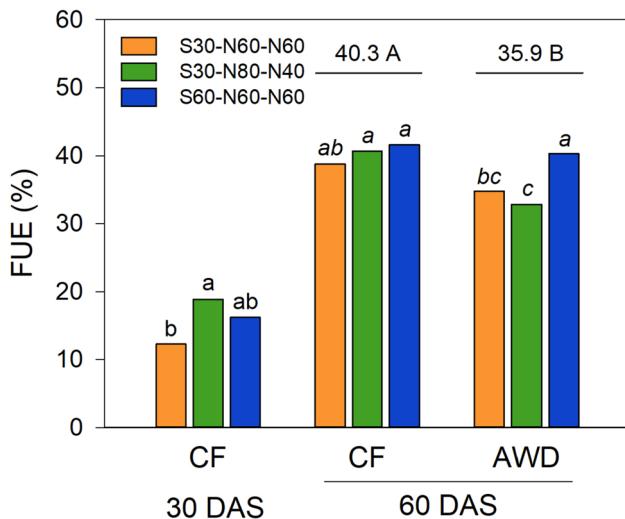


Fig. 6 Fertilizer use efficiency (FUE) as a function of water management (continuous flooding (CF); alternate wetting and drying (AWD)) and straw and fertilizer treatments (S30-N60-N60, S30-N80-N40, S60-N60-N60). The numbers at the top show the average FUE for each water management at 60 DAS with capital letters indicating statistically significant differences between averages ($p < 0.05$). Lowercase letters indicate statistically significant differences between the treatments at 30 DAS ($p < 0.05$), while lowercase italic letters indicate statistically significant difference for interaction water management*treatment at 60 DAS ($p < 0.05$)

under AWD irrigation to greater nitrification–denitrification losses typical of AWD management. Leaching losses during AWD cycles were deemed negligible as the analysis of drainage waters from the tubes showed nitrate concentrations that were below detection limits (data not shown).

Water management did not only affect the total plant N uptake but also the source partitioning of the assimilated N. Under both water managements, SDN and FDN contributed most to plant N at 60 DAS (46–64 and 34–49%, respectively), while StDN only contributed as a minimal fraction (3% for both CF and AWD), in line with the findings of Wu et al. (2022) who also reported a similar partitioning of rice N uptake under AWD. Our results agree with those reported by Chen et al. (2016) who reported that 34–42% of rice plant N was derived from fertilizer-N and 58–66% from soil N. Similarly, Hashim et al. (2015) reported FDN values for rice ranging from 20 to 35%.

Although rice plants displayed a lower N content under AWD irrigation, the FDN and consequently fertilizer use efficiency were only slightly affected by water management (Figs. 5 and 6) suggesting that the observed differences in N nutrition between different irrigations regimes were not exclusively due to higher fertilizer-N losses under AWD. In fact, Cucu et al. (2014) observed that the increased retention of fertilizer-N in flooded with respect to non-flooded soils could actually contribute to limit N losses. In light of this,

we speculate that fertilizer-N immobilization during the first 30 days of flooding could have partly limited or delayed N losses during the successive AWD redox cycles after tillering. Zhu et al. (2022) actually report a higher fertilizer-N recovery under AWD than CF, suggesting that the slightly lower FUE observed during the early growth stages in our experiment under AWD (35.9%) compared with CF (40.3%) can probably be recovered during the later growth stages allowing to reach similar or higher values of N uptake at harvest (Yang et al. 2004; Wang et al. 2016).

Unlike FDN, the fraction of SDN was greatly affected by water management, showing a significantly lower contribution to plant N nutrition under AWD (on average 14% less) with respect to permanent flooding irrigation (Fig. 5), in line with the findings of Wu et al. (2022). This is in contrast with the faster mineralization of soil organic N during the more frequent oxic soil conditions we hypothesized for AWD (Hypothesis 1). Previous studies have shown that, under predominantly anoxic conditions, Fe-reducing bacteria may use Fe^{III} in Fe oxides as an electron acceptor leading to the reductive dissolution of these Fe minerals that are also known to stabilize important amounts of organic matter. This consequently leads to the release of Fe^{II} together with substantial amounts of dissolved organic matter into solution (Said-Pullicino et al. 2014) that may serve as an important pool of labile organic N and, through mineralization, as a source of SDN for plant uptake (Deroo et al. 2021). On the other hand, the periodic fluctuations in redox conditions during AWD cycles can promote the co-precipitation of dissolved organic matter (Sodano et al. 2017), potentially enhancing its stabilization against microbial decomposition and reducing the contribution of SDN to plant nutrition. In fact, our results evidenced that whereas Fe^{II} and DOC porewater concentrations rapidly increased when soils were flooded during the first 30 DAS, the concentrations were substantially lower with the onset of AWD cycling at tillering with respect to CF (Fig. 2).

Water management only slightly influenced the contribution of StDN to plant N, nonetheless showing a lower contribution under AWD with respect to CF (Fig. 5), as previously reported by Zhang et al. (2021). Although we expected AWD cycles to promote microbial activity responsible for rice straw decomposition (hypothesis 1), the different redox conditions between the irrigation regimes could have resulted in a shift in microbial communities with different N demands (Reddy et al. 1986). In contrast to anaerobic microorganisms, aerobic microorganisms are known to have high metabolic N requirements (Gale et al. 1992; Reddy and deLaune 2008), and therefore, the faster degradation of labile organic substrates like straw under AWD (Borken and Matzner 2009) could nonetheless be associated with a slower release of StDN for plant uptake due to the enhanced microbial immobilization of N released from labile sources (Ponnamperuma 1972).

Influence of straw management on N availability and plant uptake

The timing of rice straw incorporation with respect to seeding and soil flooding was the primary driver controlling plant N nutrition during the early vegetative stages in fertilized paddy soils under both water managements and strongly influenced the source partitioning of N assimilated by the plant. Changing the time period between crop residue incorporation and the beginning of the cropping season can influence both the balance between residue N mineralization and immobilization before cropping and consequently also the availability of inorganic N forms and labile organic substrates at the time of flooding, with important implications on the availability of FDN, SDN and StDN. Indeed, we hypothesized that the anticipation of residue incorporation allows more time for the aerobic decomposition of incorporated straw before soil flooding (and the shift from a net N immobilization to a net N mineralization phase), thus enhancing the availability of StDN for plant uptake and limiting the immobilization of applied fertilizer-N during the early stages of plant development (Hypothesis 2). Results however evidenced that an early incorporation of rice straw (i.e. 60 days before seeding) substantially decreased total plant N uptake, particularly under CF (Fig. 4), suggesting that this practice did not bring the expected benefit to plant growth and nutrition. In contrast, rice straw incorporation near seeding favoured plant N uptake, especially under CF.

Source partitioning of plant N evidenced that the relative contribution of both straw- and soil-derived N was lower with early incorporation, while FDN was slightly higher but not sufficient to compensate for the lower contribution from other N sources (Fig. 5). In fact, the higher FDN and FUE with early straw incorporation were expected (hypothesis 2), because it avoids the high availability of labile organic matter in correspondence with mineral N fertilization when residues (with a C/N ratio of around 62.5) are incorporated close to seeding and therefore limits the microbial immobilization FDN to the benefit of plant uptake (Said-Pullicino et al. 2014). On the other hand, promoting straw decomposition and organic N mineralization under aerobic conditions with early incorporation negatively affected the contribution of StDN to plant uptake, falsifying our second hypothesis. This was probably because most of the plant-available StDN released before seeding was nitrified and rapidly lost by denitrification with the onset of soil flooding (Mikkelsen 1987), as well as during the successive AWD cycles. This was confirmed by the higher porewater NO_3^- concentrations at seeding (i.e. 0 DAS in Fig. 3) that were however immediately lost within 12 days from flooding.

The strongest effect on the timing of straw incorporation was however observed on the contribution of SDN to plant nutrition. Here, the incorporation of crop residues in

proximity of flooding positively affected the supply of indigenous N, particularly under CF. We explained this by considering the positive feedback straw-derived C could have on SDN availability under anaerobic conditions. Indeed, under these conditions, freshly incorporated residues serve as a source of labile substrates for the C-limited Fe-reducing bacteria, thereby promoting the reductive dissolution of Fe oxyhydroxides and release of associated organic matter into the soil solution (Marschner 2021). This was confirmed by the increasing trend and higher porewater DOC and Fe^{II} concentrations observed during the early days of plant development in soils receiving straw 30 days before flooding (Fig. 2). Desorbed (and therefore destabilized) soil organic matter can subsequently serve as an important source of indigenous N supply (Akter et al. 2018; Deroo et al. 2021), thereby improving the contribution of SDN to total plant uptake. On the other hand, anticipating the incorporation of rice straw enhances their degradation under aerobic conditions, thereby decreasing the amount of straw-derived labile C available to support microbial activity under anaerobic conditions with the onset of soil flooding (Wang et al. 2015), and consequently, the desorption of soil organic matter that can serve as a source of indigenous N supply is less pronounced. Similar effects of the timing of crop residue incorporation on the reductive dissolution of Fe oxyhydroxides and the release of Fe^{II} and soil-derived organic matter into solution were also reported in the field (Bertora et al. 2018). The positive effect of rice straw incorporation on indigenous N supply was less expressed under AWD (Fig. 5) where the regular introduction of oxygen during the redox cycling limited Fe reduction DOC desorption after tillering (Fig. 2).

Influence of fertilizer splitting on N availability and plant uptake

Sustaining plant growth through an adequate nutrient supply greatly depends on the temporal synchrony between N supply and plant demand during the different stages of crop development. In this context, the timing of fertilizer-N application and the feedback on N supply from other sources have an important bearing on N availability for microbial activity and plant uptake alike. By evaluating the effects of different fertilizer-N splitting on the source-differentiated N uptake by rice plants, we showed that applying higher fertilizer-N doses before seeding in order to temporarily favour fertilizer incorporation in the microbial biomass and limit FDN losses during the AWD cycles was not effective to increase contribution of FDN to plant N uptake or FUE (Figs. 5 and 6) over the experimental period studied, thereby rebutting our third hypothesis. We cannot however exclude that the benefits of a high fertilization dose at seeding under AWD are eventually observed at the later stages of plant development and that the release of immobilized fertilizer-N can

actually contribute to plant N uptake after 60 DAS (beyond our experimental period) due to the higher N demand of the aerobic microbial population (Somaweera et al. 2016). This aspect warrants further investigation. There was however a slight but significant positive effect on root development under flooded conditions, as previously observed by Yang et al. (2021).

Higher fertilization doses at seeding did however enhance the contribution of SDN, and to a much smaller extent StDN, to plant uptake at 30 DAS (Fig. 5). This actually led to a 17% increase in the contribution of SDN to total plant N uptake by 60 DAS under CF, but no significant difference was observed with respect to StDN (Fig. 5). We postulate that the greater root biomass observed for this N fertilizer split ratio (Table 3) could have also promoted belowground C allocation in the form of rhizodeposited C, thereby resulting in microbial activation and a positive rhizosphere priming effect on soil-derived organic matter mineralization, similar, but to a lesser extent, to what was observed with rice straw incorporation. Luo et al. (2019) have shown that N fertilization can increase the allocation of plant photosynthates into the rice rhizosphere as a result of a higher root biomass. In addition, Zhu et al. (2018) and Jiang et al. (2021) have shown a relationship between root C exudation, C (and N) availability for microbes and a positive rhizosphere priming at high N fertilization rates (as those used in this experiment). In fact, the combination of enhanced fertilizer-N uptake and increased root C exudation by the plant may induce a strong increase in competition between plants and microorganisms for N inducing N limitation in the rhizosphere which induces microbes to accelerate the mineralization of SOM to obtain nutrients.

On the other hand, the relative contribution of SDN to total plant N under AWD was slightly but significantly higher when N fertilizer dose was split equally between pre-seeding and tillering suggesting that a more regular temporal distribution of fertilizer-N could favour microbial activity and indigenous N supply. These findings further suggest that the added-N interaction of N fertilization on soil-derived N uptake in rice paddies may not only depend on the fertilizer-N input rates (Sun and Zhu 2022) but also on soil redox conditions.

Conclusions

The widespread adoption of AWD water management in rice paddies to improve the water use efficiency and environmental sustainability of rice cropping systems will depend on avoiding yield gaps with respect to the conventional continuous flooding practices. Providing adequate N supply for rice plants under AWD, particularly during the early vegetative stages, is one of the most pressing challenges.

N supply from different sources depends on the complex interactions between water, fertilizer and crop residue management which need to be specifically optimized to enhance plant N uptake. In this study, we provide important insights into the influence of management practices on the source partitioning of plant N uptake. The main findings of this work can be summarized as follows:

- 1) Soil-derived N was the main source of N for rice plants at panicle initiation stage (46–64%), followed by fertilizer-derived N (34–49%), while straw-derived N only contributed minimally (<3%). Despite the low contribution of crop residues to plant nutrition, their incorporation can play a crucial role in enhancing soil N supply by promoting the positive feedback on soil organic matter desorption under anaerobic conditions that can in turn serve as an important pool of labile organic N and a source of SDN for plant uptake.
- 2) Although AWD reduced total N uptake by about 4–25% with respect to continuous flooding, this could only be partly attributed to higher fertilizer-N immobilization or losses as a result of redox cycling, suggesting that other N sources were affected by water management. In fact, the contribution of SDN to plant N uptake was strongly related to redox conditions, with a higher soil N supply observed under continuous flooding, particularly when straw was incorporated in proximity to flooding (61–64% of total plant N). Indeed, the combination of a fresh organic matter supply and reducing conditions under continuous flooding favoured the reductive dissolution of Fe oxyhydroxides and the desorption of soil organic matter that presumably increase soil N supply via mineralization.
- 3) Under continuous flooding, higher N fertilization doses at seeding may also enhance organic matter decomposition, thereby priming soil N supply, although the opposite was true under AWD probably due to the different metabolic N requirements of the microbial populations. From an agronomic point of view, an equilibrated splitting of N fertilizer between pre-seeding and tillering stages could favour microbial activity under AWD improving N supply from straw and soil organic matter degradation.

Although our study has highlighted how management practices may modulate the contribution of different N sources to plant nutrition, most of these effects are a result of changes in plant–microbe interactions in the rhizosphere that are not always unequivocal. This warrants further research to understand how these interactions are influenced by changes in soil redox conditions and their implications on plant nutrition, in order to provide useful indications for N management in rice paddies.

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Data Availability The data will be available on request.

Declarations

Competing interests The authors declare no competing interests.

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