Quantification of plant water uptake by water stable isotopes in rice paddy systems

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REGULAR ARTICLE

Quantification of plant water uptake by water stable isotopes in rice paddy systems

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Abstract
Aim Understanding the source water utilization of rice-based cropping systems helps develop improving water management strategies for paddy management. We investigated the effects of altered flooding regimes and crop diversification on plant root water uptake on a fully-replicated field trial at the International Rice Research Institute in the Philippines.
Methods All potential water pools, e.g., plant and soil extracted water, were analyzed for their water stable isotopic compositions (δ^2H and δ^{18}O). We determined the relative contributions from different water sources to root water uptake (RWU) of rice plants by applying a multi-source mixing model (Stable Isotopes Analysis in R, SIAR). The sensitivity of the model to the incorporation of prior information based on in-situ measurements of soil water content and root length density was investigated as well.
Results The modeling results showed that wet rice plants mainly extracted surface ponded water (~56–72%) during both wet and dry seasons followed by soil surface (0–0.02 m) water (~17–19%) during growth. Dry rice extracted ~40–50% of its water from shallow soil (0–0.5 m) and ~35% from 0.1 to 0.3 m depth when the plants were matured.
Conclusions The mixing model results were better constrained with the additional information on soil water content and root length density. The relative contributions of the soil water sources to RWU decreased with depth and reflected the exponential shape of the root density profile. The main water source for wet rice was surface ponded water (independent of the season), whereas shallow soil water was the main source for dry rice.

Keywords Water stable isotope · Rice · Root water uptake · Multi-source mixing model · Prior information · Sensitivity analysis · Plant water enrichment · Water extraction

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Introduction

In recent years, the analysis of the stable isotopic composition of water (δ^2H, δ^{18}O) in plants and soils has shown potential in improving our understanding of eco-hydrological processes (Sprenger et al. 2016) and in particular of plant root water uptake (RWU) (Rothfuss and Javaux 2017).

Soils are complex hydrological systems regulated by precipitation, infiltration, interflow, groundwater recharge, and evapotranspiration (Vereecken et al. 2016). How these processes prevail and interact, and are associated or not with isotopic fractionation, defines the isotopic composition of soil water. Apart from some exceptions (Ellsworth and Williams 2007; Zhao et al. 2016), no isotopic fractionation is generally observed during RWU (e.g., Zimmermann et al. 1967). Assuming a perfect mixing of water in the xylem vessels, the isotopic composition of the water extracted by the root system can be therefore conceptualized as a mixture of the isotopic compositions of different potential water sources weighted by the sources' contributions to RWU (Midwood et al. 1998; February et al. 2007; Brooks et al. 2010; Bijoor et al. 2012).

RWU of different plants, including trees (e.g., Edwin et al. 2014; Beyer et al. 2016), shrubs (e.g., Wu et al. 2014), maize (e.g., Zhang et al. 2011a), winter wheat (e.g., Fengrui et al. 2000; Zhang et al. 2011b), and cottonwood (e.g., Flanagan et al. 2017) have been analyzed in the past. Although research was conducted on the RWU patterns of rice (e.g., Lu et al. 2002; Bello et al. 2004; Henry et al. 2012; Wang et al. 2017), only a few studies applied water stable isotopes at the field scale (Shen et al. 2015). Therefore, the magnitude and dynamics of rice RWU during an entire growing season remains largely unexplored.

Mixing models can be applied to determine the sources' contributions to plant RWU (Tang and Feng 2001; McCole and Stern 2007; Wang et al. 2010a). This has been done for crops such as maize (Zhang et al. 2011a) and rice (Shen et al. 2015). The most commonly used models are those of Parnell et al. (2010, 2013); Phillips and Gregg (2003). Bayesian approaches provide quantitative estimates (along with their uncertainties) of the relative contributions of soil water sources to RWU based on δ^2H and δ^{18}O compositions (Cramer et al. 1999; Burgess et al. 2000; Phillips and Gregg 2001). Recently, Rothfuss and Javaux (2017) discussed the advantages and drawbacks of the different model approaches. Shen et al. (2015) successfully applied a mixing model by Phillips and Gregg 2003 to quantify water sources' relative contributions to rice plant growth, but no study has been able to successfully integrate additional observations, such as root information (e.g., root length density, RLD) and soil water content (SWC), into mixing model calculations. Considering root activity and information on root depth and distribution are also highly beneficial for plant RWU calculations (Schenk 2008; Kulmatiski et al. 2010). This will contribute improving the prediction of the rice grain water δ^{18}O which can be used a as proxy for the geographical origin of the rice cultivar (Chung et al. 2016) and also as an indicator of physiological changes in response to air temperatures (positive correlation in night) during rice grain filling (Akamatsu et al. 2014).

Rice (*Oryza sativa L.*) is the dominating staple food for nearly half of the world's population (Maclean et al. 2002), but at the same time, it is one of the most water-consuming grain crops (Janssen and Lennartz 2007). Rice crops use approximately 30% of all freshwater worldwide and over 45% of the freshwater consumed in Asia (Maclean et al. 2002). An estimated 3000–5000 L of freshwater is required to produce just one kilogram of rice grains (Alexandratos and Bruinsma 2012). Rice is extremely sensitive to soil water conditions. To ensure sufficient water volume, farmers maintain flooded conditions in the most well-known traditional rice production system (wet, lowland, or anaerobic production system). Water use is high in this system compared to any other rice-based production system (Peng et al. 2006).

In wet rice production systems, the most common starting procedures are transplanting and direct seeding, during which the fields are continuously flooded with a water level of 0.05–0.1 m. This water level is kept throughout the growing season. However, it is not necessarily required to flood the rice with high water levels to ensure high grain yields and quality (Borrell et al. 1997). Wet rice fields often have poor drainage systems and shallow groundwater tables (Yang et al. 2004), causing limited vertical root growth due to an unfavorable physio-chemical environment in the soil (Zhang et al. 2017). Adoption of an appropriate water management system is therefore crucial for improving rice root growth (Sahrawat 2000) to sustain rice production, especially in regions where water availability is limited (Mueller et al. 2012). This can be accomplished by understanding the dominant depths of RWU at different maturity stages. The dry rice (also referred to as non-flooded, upland, or aerobic) production system, which we investigated in our study, is one approach used as a local solution to save water in regions where water is limited. However, with this approach, yields are smaller compared to flooded rice production systems (Bouman 2007). The development of new water-saving production systems (Uphoff and Randriamiharisoa 2002; Belder et al. 2004) would not only save water but also improve the economic value of the rice produced. Therefore, apart from improvements in water productivity (defined as grain yield divided by the amount of system's water input (Tuong and Bhuiyan 1999; Bouman et al. 2005)) by plant breeding (Bernier et al. 2008; Luo 2010), there is also the possibility to reduce unproductive water use at the expense of a moderate yield reduction (Passioura 2006). Achieving better management of water resources and increasing rice production without raising the consumption of additional freshwater resources requires a more-detailed understanding of water cycling in rice-based cropping systems (Heinz et al. 2013).

This study examined soil and plant water isotopic composition data during wet and dry rice cultivation to localize the mean root water depth and to quantify the relative contributions of soil water sources to plant RWU by (i) direct graphical inference and (ii) using the multi-source mixing model SIAR (Parnell et al. 2013) following the *modus operandi* of Rothfuss and Javaux (2017). To improve the mixing model performance, we incorporate additional information on RLD and SWC. This information can help expand our understanding of water flux partitioning mechanisms with regard to different irrigation scheduling (flooded and non-flooded) for different production systems (wet and dry rice) during different climatic conditions (wet and dry seasons). Finally, we calculated water productivity in order to evaluate the production systems that achieve efficient water management.

Material and methods

Study area and experimental design

The experiment was conducted at the experimental lowland farm (14° 11' N, 121° 15′ E, 21 m a.s.l.) of the International Rice Research Institute (IRRI) in Los Baños, Laguna, Philippines. The average total rainfall during the wet season (WS) from June to November is roughly 1700 ± 50 mm and 300 ± 25 mm in the dry season (DS) from December to May. The mean annual temperature is 27.1 ± 3 °C (Data from IRRI Climate Unit, 2016). The soil type is classified as an *Andaqueptic Haplaquoll* (USDA classification), containing mostly silty clay (Table 1).

Texture and mineralogical analyses of the soil were carried out at the Institute of Soil Sciences and Soil Conservation (Justus Liebig University Giessen, Germany). The clay fraction mainly consists of mainly vermiculite, kaolinite and smectite. The soil has an average bulk density of 1.5 ± 0.2 g cm^{-3}, a depth of up to 0.3 m, an average pH of 6.1 ± 0.2, and an organic carbon content of 1.8 ± 0.1% (Weller et al. 2015).

The experiments were conducted in the WS 2015 and DS 2016. During the WS, all fields ($n = 9$) were cultivated with wet rice (cultivar NSIC Rc222). During the DS, the fields labeled R-WET ($n = 3$) were cultivated with wet rice again, while R-MIX fields (n = 3) were cultivated with dry rice (cultivar NSIC Rc192), and M-MIX (n = 3) fields were cultivated with maize. Each field was homogeneously cultivated with one crop type and subjected to the same water and nutrient management regime. A total of 130 kg N ha^{-1} urea was applied over three fertilization dates (30/50/50 kg N ha^{-1}) during both seasons. Each field contains three plots each with different treatments, i.e., straw incorporation to the soil (S), straw plus mung bean as an inter-crop in the dry to wet transition period (M), and a control plot (C).

For our experiment, plots with mung bean treatment (M) were excluded only during the DS and M-MIX fields were excluded during both seasons due to different crop management, resulting in a total of 18 plots during WS and 12 plots during DS. The plot sizes varied between 170 and 190 m^2. Each plot was separated by bunds reinforced with plastic sheets to avoid lateral flow between plots. Irrigation water was supplied by a hydrant system from a nearby reservoir, which was filled

Table 1 Soil texture of different depths along the soil profile

Soil depth [m]	Texture		
	Clay (%)	Silt (%)	Sand (%)
0–0.10	58.3	33.4	8.4
0.10–0.20	59.5	30.9	9.7
0.20–0.40	58.9	29.6	11.5
0.40–0.60	50.0	26.7	23.4

with pumped groundwater and sometimes included rainwater. Two air-conditioned field containers housed our analytical instruments (Heinz et al. 2013). Transplanting and harvest dates were Jul. 21st and Oct. 30th during the WS 2015, respectively, and, Jan. 8th and Apr. 10th, during the DS 2016, respectively.

Water management

All fields were flooded for the initial land preparation, which consisted of four phases: (1) land soaking and straw incorporation at straw fields, (2) plowing, (3) harrowing, and (4) a second straw incorporation at straw fields, ending with a final leveling for transplanting (Datta 1981). Wet rice fields were kept under traditional irrigation management, maintaining water saturated soil conditions throughout most of the growing period. Water was drained during the first 2 weeks after transplanting. Afterward, fields were kept flooded with 0.02–0.1 m water level until 2 weeks before harvest. Dry rice fields were only irrigated when weather conditions suggested a severe drought risk (this occurred 4–5 times during the DS).

Rainfall was higher during the WS than DS; therefore the total irrigation was lower during the WS than the DS (Fig. 1). The total irrigation amount for R-WET fields was 470 mm/field during the WS and increased to 1270 mm/field during the DS, where R-MIX fields were each irrigated with 517 mm of water. The total irrigation for all the fields was 526 mm/field during the WS and 640 mm/field during the DS. Irrigation in the WS mainly depended on precipitation amounts where irrigation was only applied to maintain flooded conditions. Surface ponded water (SW) and groundwater (GW) levels were measured during the entire sampling period with capacitance loggers (Water Level Capacitance Loggers, Odyssey Dataflow System, Christchurch, New Zealand) using 2 m cable lengths for GW and 0.5 m cable lengths for SW measurements from the surface level (0 m). The logger had a resolution of approximately 0.8 mm. Water levels were recorded every 15 min.

Soil, plant, and water sampling

Soil samples were collected from vertical profiles at nine different depths down to 0.6 m (0, 0.05, 0.1, 0.15, 0.2, 0.2–0.3, 0.3–0.4, 0.4–0.5, 0.5–0.6 m) at each plots during the three main growing stages as described by Counce et al. (2000): vegetative stage (GS1), which runs from germination to panicle initiation, reproductive stage (GS2), which runs from panicle initiation to flowering, and ripening stage (GS3), which runs from flowering to maturity (Fig. 1).

During each growing stage and throughout both WS and DS, we sampled altogether 90 soil profiles, which gave a grand total of 810 soil samples. Soil samples were collected and stored in sealed

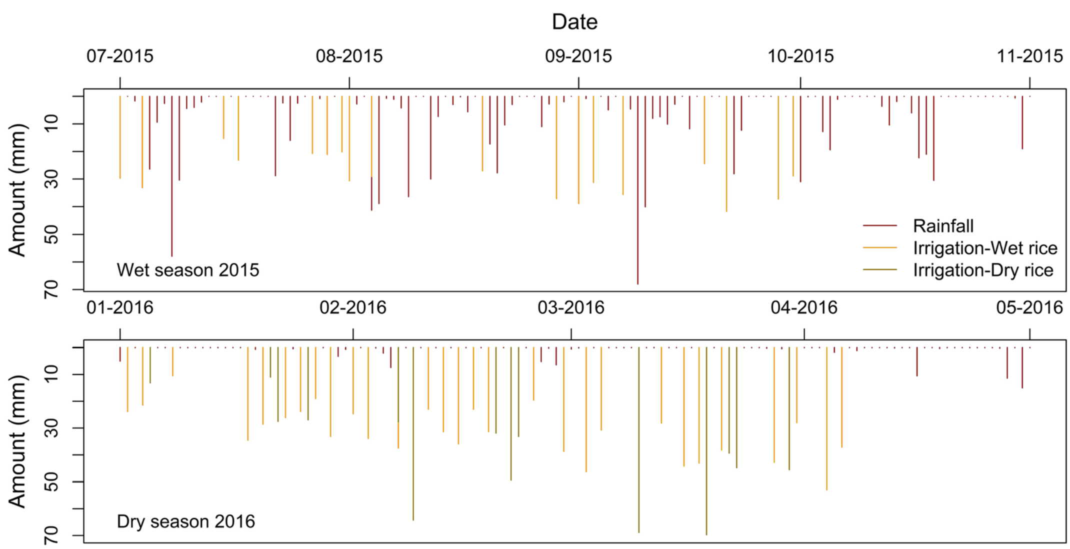

Fig. 1 Temporal variation of rainfall and irrigation water inputs of wet and dry rice fields for the wet season 2015 (top) and dry season 2016 (bottom)

aluminum bags (Weber packaging, Güglingen, Germany, CB400-420BRZ, 80 mm × 110 mm), while plant samples were kept in brown glass bottles (Labsolute Gewindeflaschen, Th.Geyer, Germany, ND24, 40 mL) sealed with Parafilm®. Samples were immediately placed in an ice-filled Styrofoam box until taken to the laboratory where they were kept frozen.

Soil and plant stem samples were extracted by cryogenic vacuum extraction (Orlowski et al. 2013) at the Institute for Landscape Ecology and Resources Management (Justus Liebig University Giessen, Germany). Extraction conditions were set depending on the sample type. Soil samples were extracted for 4 h at 200 °C using a sand bath to heat the samples, while plant samples were extracted for 3 h at approximately 95 °C using a water bath to heat the samples.

We took 10 to 15 g of soil samples from the aluminum bags for the determination of gravimetric soil water content. This was based on the weight loss following cryogenic water extraction. Note that these values are therefore different from the soil water contents as commonly determined in the field via soil core sampling and subsequent gravimetric determination or volumetric soil water sampling. However, they remain representative of the vertical heterogeneity that is observed in-situ.

A rainwater (RW) collector with a funnel width of 0.3 m diameter was installed on top of our field analytical container and covered with a mosquito net to avoid contamination. This collector was connected to a sampling bottle (1 L polypropylene) inside an air-conditioned container to reduce evaporation. Irrigation water (IW) were collected directly from the irrigation pipe during irrigation events. The amounts of rain and irrigation events are shown in Fig. 1. SW and GW were collected weekly from each plot at existing sampling stations (Heinz et al. 2013). All water samples were collected in 50 mL plastic bottles (Nalgene) following IAEA standard procedures (Newman et al. 2009).

Rice root sampling and analysis

Root samples were collected simultaneously with soil samples using the same sampling corer (length is 0.6 m and diameter is 0.05 m) down to a depth of 0.6 m. Roots were washed, scanned, and analyzed using the winRHIZO software (WinRHIZO 1991) for RLD (cm cm^{-3}) in the plant physiology lab of the IRRI (Fig. 2).

Isotopic measurements

Hydrogen and oxygen isotopic compositions of water samples were measured via off-axis integrated cavity output spectroscopy (OA-ICOS, DLT-100-Liquid Water Isotope Analyzer, Los Gatos Research Inc., Mountain View, CA, USA) and reported in permil on the international scale (δ^2H and δ^{18}O). Isotopic composition data of all water source types were checked for spectral interferences using the Spectral Contamination Identifier (LWIA-SCI) post-processing software (Los Gatos Research Inc.). Plant samples that were marked for ethanol (EtOH) and methanol (MeOH) contamination, were re-analyzed by the DELTA V Advantage isotope ratio mass spectrometer (IRMS) with ConFlo IV Interface coupled to a TC/EA pyrolyzer equipped with an AS 3000 II Autosampler. Analytic precisions for δ^{18}O and δ^2H were 0.2 ‰ and 0.6 ‰ for the DLT-100, and 1.0 ‰ and 1.6 ‰ for the IRMS, respectively.

The global meteoric water line (GMWL) was determined following Rozanski et al. (1993) while the Local Meteoric Water Line (LMWL) was defined as $\delta^2H = 7.52*\delta^{18}O + 5.86$, according to the local precipitation isotopic composition data collected during the reference period 2000–2015 (GNIP-IAEA 2016). Linear correlations in a dual isotope coordinate system (δ^{18}O, δ^2H) were calculated for each data cluster (e.g., water, soil, and plant).

Statistical analysis

Data were tested for normal distribution using the Shapiro-Wilk test and for homogeneity of variances using the Fligner-Killeen test (Python 2.7.10.0). We then tested for statistically significant differences of water isotopes (δ^2H and δ^{18}O) between all water sources during growing stages, seasons, and treatments. In order to test these differences, the non-parametric rank-based Kruskal-Wallis test was applied, because the data were not normally distributed. We rejected the null hypothesis that two profiles were significantly different with $p \leq 0.05$. A correction for commonalities in the data was considered. In this case, the rank-based test statistic that takes no ties into consideration was rescaled by a factor,

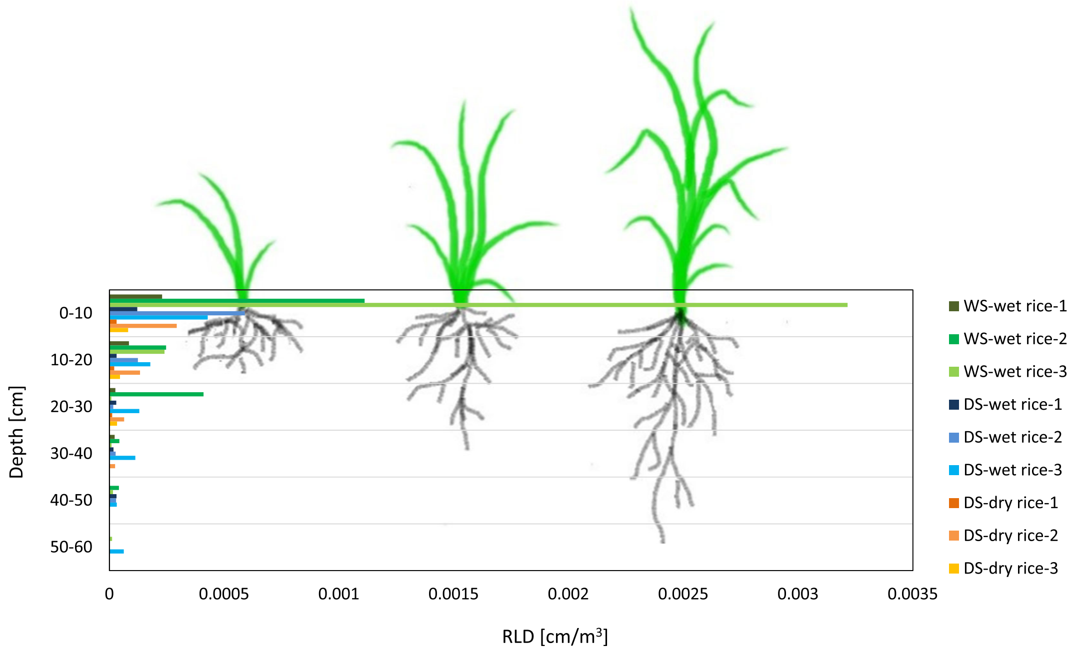

Fig. 2 Root length density (RLD, cm cm^{-3}) profiles for the vegetative (GS1), reproductive (GS2) and ripening (GS3) growing stages of wet rice (wet) in wet season 2015 (WS) and wet rice as well as dry rice (dry) in the dry season 2016 (DS)

which depends on the number of tied observations and the number of observations in all samples combined (Kruskal and Wallis 1952).

Direct inference method

The mean RWU depth (Z) was graphically determined as the depth where the soil water isotopic composition equals that of the stem water (direct graphical inference method). This model makes the assumption that, instead of a vertically distributed root system, there is one single root sampling at a single depth at a time.

Multi-source mixing model

The distribution of the relative contributions of the soil water sources to RWU was estimated using the multi-source Bayesian mixing model SIAR (Stable Isotope Analysis in R, Parnell et al. 2010), which is available as a R package (https://cran.r-project.org/web/packages/siar/index.html). This provides a distinct advantage over the direct graphical inference method (Brunel et al. 1997) as it analyzes the isotopic composition data systematically and provides quantitative estimates of uncertainties for each source's relative contributions, although some diffuse patterns of frequency distributions may be difficult to interpret.

Model input data

SIAR requires as input variables the plant potential water sources and stem water δ^2H and δ^{18}O compositions. Prior to the analyses, the different water sources were (i) identified and (ii) their representative isotopic compositions calculated. Both points relied on the following assumptions: (i) soil water across depths and SW were the designated potential sources, i.e., IW, RW, and GW were excluded from the analysis; especially GW levels were lower than the maximum root distribution (>0.6 m), (ii) the isotopic compositions of the soil water sources were obtained from the raw isotopic compositions (δ_S / ‰) and SWC values (cm^3 cm^{-3}) profiles using the following equation;

$$\delta_{S,J}(z_J) = \frac{\sum_{j \le J} \delta_S(z_j)^* SWC(z_j)^* \Delta z_J}{\sum_{j \le J} SWC(z_j)^* \Delta z_j} \quad (1)$$

where z_J (cm) and z_j (cm) refer to the depth of the J^{th} soil water source and of the j^{th} sampling location, respectively. Equation (1) translates raw, isotopic information (measured at depth j) into representative isotopic compositions of the different sources. Soil water δ^{18}O and δ^{2}H translated profiles were used to compute the deuterium excess (d-excess) calculated as $d = \delta^{2}\text{H} - 8{*}\delta^{18}\text{O}$ (Dansgaard 1964). The standard error associated with the calculation of d was determined using an extension of the formula proposed by Phillips and Gregg (2001) (Rothfuss et al. 2010).

Model setup

An important feature of the Bayesian model is the definition of the initial set of frequency distributions of the different sources' relative contributions to RWU. The final set of frequency distributions determined by the model after a determined number of runs strongly depends on this "prior information". The sensitivity of SIAR to the definition of this prior information was investigated by running the model in two different ways. First, the model was run with non-informative (i.e., "flat") priors. In this configuration, the relative contribution of each potential water source to RWU had an initial frequency distribution which was normally distributed around $1/n$ (where n is the number of sources). Second, the model was run with "informative priors", i.e., by taking into account additional information on RLD and SWC. This should better constrain the model and provides physically-sound estimates of relative RWU profiles. These priors were normally-distributed around p_J, the value of the relative variable RLD*SWC for source J:

$$p_J = \frac{\mathrm{RLD}(z_J)^{*}SWC(z_J)}{\sum_J \mathrm{RLD}(z_J)^{*}SWC(z_J)} \tag{2}$$

Equation (2) implies that the probability that the source is actively contributing to RWU is higher where SWC or RLD is higher, and vice versa. For SW, RLD was fixed equal to that of the uppermost soil water source, and SWC was set to 100%. In addition, potential sources were removed from the analyses with informative priors (RLD and SWC) due to low root presence (especially the depths of 0.4–0.6 m during GS1 and, 0.5–0.6 m during GS2 of all crops during both seasons).

Results

Informative priors

More than 60% of the RLDs were concentrated in the top 0.1 m during all growing stages (Fig. 2). A substantial portion of the root length (15–25%) was found at 0.2–0.3 m during GS2 and GS3. At GS3, the vertical roots were distributed down to 0.6 m, and lateral distribution was highest at a depth of 0–0.1 m. All rice plant roots in this study had denser distributions in the topsoil than the deeper soil during both WS and DS. The root system of wet rice during GS1 showed a shallow distribution, but from GS2 to GS3, the root system developed deeper down to a depth of 0.5–0.6 m even though the root density is higher at shallow depth. Dry rice roots during GS1 reached down to 0.2 m. When the plants matured, the roots grow deeper down to 0.3 m. During GS3, roots were found down to a depth of 0.4–0.5 m (Fig. 2).

Wet rice had higher SWCs than dry rice. Surface soil had a SWC of 15.2 ± 2.7% in WS, which remained within the same range throughout the season. Nevertheless, below 0.1 m depth, SWC values spread over a similar range (13.1 ± 1.9%) until the 0.6 m depth, which was less than the surface soil water. Throughout the DS growing period, SWC was high at the surface for wet rice, equal to 17.7 ± 1.2% at the surface, and decreased down to 12.0 ± 1.3% lower in the profile. The highest SWC values for dry rice were observed at 0.05 m (12.0 ± 1.0%) and remained around 11.8 ± 1.2% below 0.05 m.

Isotopic compositions of water sources

Figure 3 displays in a dual isotopic (δ^{2}H,δ^{18}O) coordinate system soil water samples taken at 0–0.2 m and 0.2–0.6 m depth, SW, GW, RW, and IW samples, and plant stem water samples (with standard deviations). The GMWL and LMWL were plotted as well for comparison with respective regression lines of the water sources. Soil water δ^{2}H and δ^{18}O were higher in wet rice profiles, especially for the upper layers. Soil water isotopic composition during the WS was significantly different from GW, SW and RW ($p < 0.04$), but not different from IW ($p = 0.3 \pm 0.2$).

The slope of the linear regression relationship of soil water samples (δ^{2}H, δ^{18}O) in the referential changed from

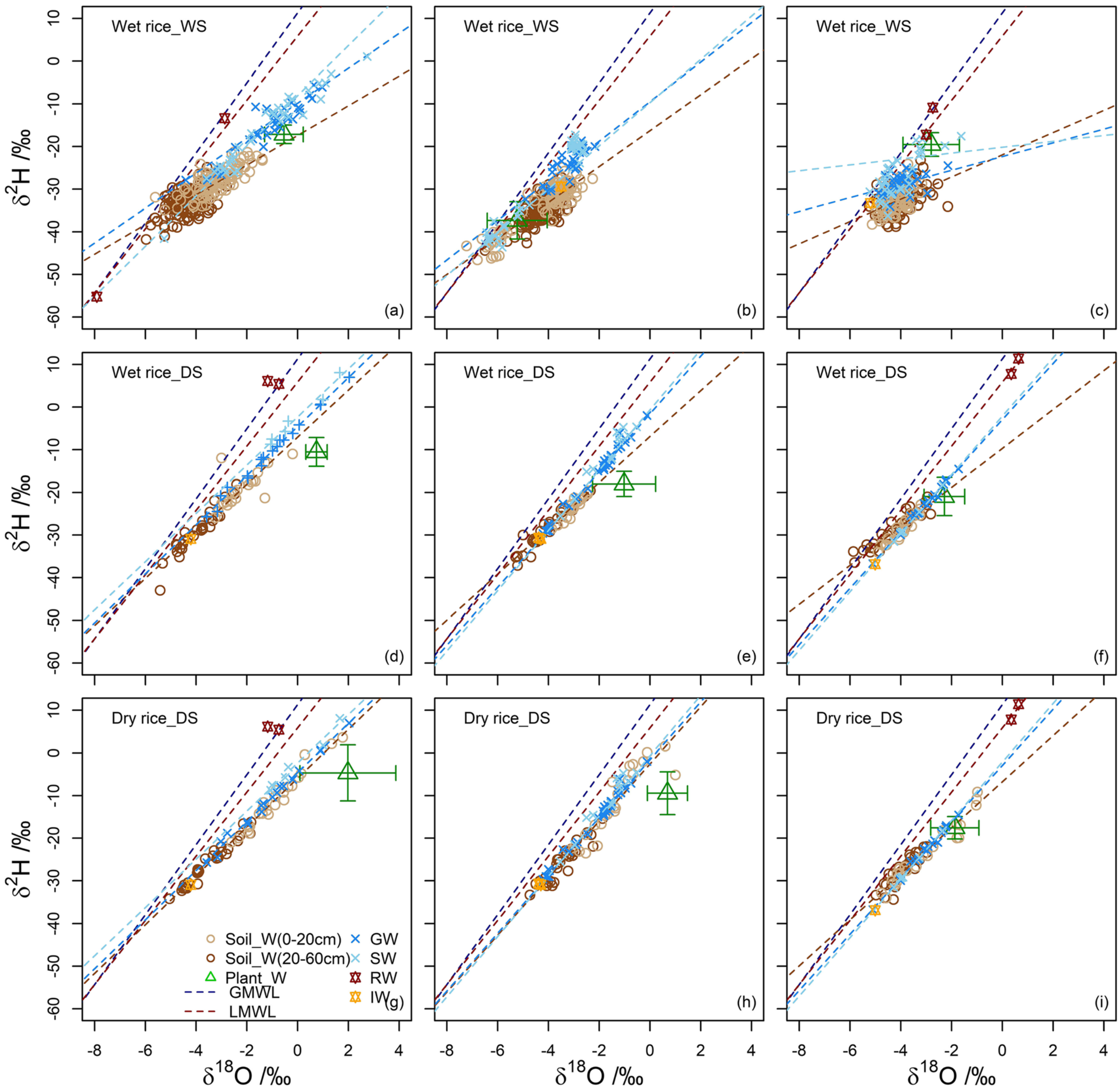

Fig. 3 Dual (δ^{18}O, δ^{2}H) isotope plots of plant stem water, soil water 0–0.2 m, soil water 0.2–0.6 m, and other water sources (groundwater (GW), surface water (SW), rain water (RW), and irrigation water (IW) from growing stage 1 (GS1, 1st column; **a, d, g**), growing stage 2 (GS2, 2nd column; **b, e, f**), and growing stage 3 (GS3, 3rd column; **c, f, i**) from wet rice during the wet season 2015 (1st row; **a, b, c**), wet rice during the dry season 2016 (2nd row; **d, e, f**), dry rice during the dry season 2016 (3rd row; **g, h, i**) in comparison to the local meteoric water line (LMWL) and global meteoric water line (GMWL)

3.5 to 4.2 and to 2.6, during the plants' growth from GS1 to GS2 and to GS3 in wet rice during the WS. Slopes values (>4.5) and coefficient of determination ($R^2 > 0.85$) were higher during the DS than the WS. Slopes values were higher for dry rice (average = 6.0, $R^2 > 0.92$) than for wet rice (average = 5.2, $0.85 < R^2 < 0.94$).

The average RW δ^2H (respectively δ^{18}O) varied from WS to DS from −17.6 ± 10.1 to 8.8 ± 2.2 ‰ (−3.2 ± 1.5 to −0.3 ± 0.8 ‰) (Fig. 3). During the same seasons, IW δ^2H and δ^{18}O varied from −32.0 ± 3.2 to −34.6 ± 3.5 ‰ and from −4.3 ± 0.6 to −4.9 ± 0.5 ‰, respectively. GW and SW showed relatively similar ranges during both seasons with no statistically significant differences for δ^2H ($p = 0.35$) or δ^{18}O ($p = 0.67$). From WS to DS, SW and GW δ^2H and δ^{18}O ranged from −24.1 ± 7.3 to −31.5 ± 4.27 ‰ and − 3.2 ± 1.7 to −3.3 ± 0.4 ‰, respectively. Both δ^2H and $\delta^{18}O$ values were higher at the beginning of the DS and decreased towards the end of the WS. During the DS, wet rice fields (Fig. 3d–f) showed lower GW isotopic composition values ($\delta^2H = -14.2 \pm 7.5$ and $\delta^{18}O = -1.7 \pm 1.3$ ‰) than dry rice ($\delta^2H = -11.8 \pm 8.6$ and $\delta^{18}O = -1.3 \pm 1.5$ ‰) (Fig. 3g–i). Slopes of both GW and SW during the WS were around 4.4 and increased to 6.3 during the DS with a very high correlation ($R^2 = 0.99$, Table 2). SW was isotopically more enriched than IW (which was also a mixture of RW and GW from the surrounded area), especially during the WS. The IW isotopic compositions were significantly different from those of SW and GW ($p < 0.003$) for both hydrogen and oxygen. During the WS, there was no statistically significant difference of $\delta^{18}O$ values between RW on the one hand and GW ($p = 0.82$) or SW ($p = 0.71$) on the other hand. However, the contrary was observed for δ^2H ($p < 0.003$). We observed fluctuation of groundwater levels in all fields between 0.2 and 0.6 m below the surface during the WS, while it had been gradually lowered during the DS below 0.6 m.

The isotopic composition in rice plant stem water was more heterogeneously-distributed in dry rice fields than wet rice, especially during GS1. The dry rice stem water was isotopically more enriched than the wet rice water during the DS (Fig. 3g–i), though plant water was isotopically more enriched during the DS than the WS overall. The wet rice stem water δ^2H and $\delta^{18}O$ measured

Table 2 Slope value and standard error, coefficient of determination (R^2) of the $\delta^{18}O$ vs. δ^2H linear regression for each water pool (i.e., soil water, surface water and groundwater) in vegetative, reproductive and ripening stages (GS1, GS2, GS3) during both wet (WS) and dry (DS) seasons

Season, GS	Crop	Water type	slope	Std-error	R^2	*p*-value
WS-GS1	Wet rice	Soil water	3.48	0.17	0.63	2.2E-53
WS-GS2	Wet rice		4.21	0.17	0.72	9.9E-68
WS-GS3	Wet rice		2.61	0.38	0.23	1.4E-10
DS-GS1	Wet rice		5.52	0.28	0.88	1.7E-25
DS-GS2	Wet rice		5.38	0.19	0.94	1.1E-32
DS-GS3	Wet rice		4.57	0.27	0.85	5.4E-23
DS-GS1	Dry rice		5.72	0.10	0.98	2.3E-48
DS-GS2	Dry rice		6.69	0.26	0.93	1.7E-31
DS-GS3	Dry rice		5.39	0.22	0.92	6.3E-30
WS-GS1	–	Surface water	5.88	0.46	0.91	9.3E-10
WS-GS2	–		5.07	0.50	0.87	2.0E-08
WS-GS3	–		0.69	0.28	0.28	2.8E-02
DS-GS1	–		6.29	0.47	0.99	2.8E-04
DS-GS2	–		7.06	0.32	0.99	2.4E-05
DS-GS3	–		6.86	0.11	1.00	4.2E-07
DS-GS1	–		6.29	0.47	0.99	2.8E-04
DS-GS2	–		7.06	0.32	0.99	2.4E-05
DS-GS3	–		6.86	0.11	1.00	4.2E-07
WS-GS1	–	Groundwater	4.10	0.43	0.85	6.4E-08
WS-GS2	–		4.64	0.87	0.64	6.6E-05
WS-GS3	–		1.61	1.01	0.14	1.3E-01
DS-GS1	–		6.16	0.13	0.99	5.2E-18
DS-GS2	–		6.78	0.16	0.99	6.3E-18
DS-GS3	–		6.59	0.17	0.99	3.2E-17
DS-GS1	–		6.16	0.13	0.99	5.2E-18
DS-GS2	–		6.78	0.16	0.99	6.3E-18
DS-GS3	–		6.59	0.17	0.99	3.2E-17

during the WS were significantly different from all other water sources ($p < 0.001$) (Fig. 3a–c), except for RW during GS3 ($p = 0.3$) (Fig. 3c). During the DS, plant stem water isotopic compositions were significantly different from all other water sources, except during GS3. During GS3, the plant water isotopic compositions did not significantly change from SW to GW ($p > 0.1$). They decreased as the plants grew, especially during the DS. During the WS, lower isotopic composition values were measured during GS2, whereas higher values were observed during GS3 (Fig. 3b–c).

Relative RWU profiles

Figures 4, 5 and 6 display the d-excess of plant stem water, of the potential soil water sources, and of irrigation water (IW), ground water (GW), and surface ponded water (SW) (1st rows (a, d, g)) for each growing stage (GS1 to GS3) of wet and dry rice during the WS and DS. Results of the SIAR model, i.e., the range (shaded areas) and most frequent value (MFV, black step like line) of the sources' relative contributions, are reported with either flat or informative priors (2nd (b, e, h) and 3rd (g, h, i) rows). D-excess combines in a dual isotopic co-ordinate system the $\delta^{18}O$ and $\delta^{2}H$ isotopic compositions, and gives a proxy for SIAR input data; therefore, d-excess along with its calculated standard error, are shown with the SIAR results while the soil water $\delta^{18}O$ and $\delta^{2}H$ profiles are reported in Appendix. Although there may not be any overlap between sources and plant water $\delta^{18}O$ or $\delta^{2}H$ isotopic compositions when considering the 95% confidence intervals, there was an overlap between sources and stem water d-excess (1st row in Figs. 4, 5 and 6).

Results with flat priors (2nd row in Figs. 4, 5 and 6) showed very similar ranges of density distribution (0.40 ± 0.03, 0.42 ± 0.05, 0.46 ± 0.05) and nearly constant MFVs (0.10 ± 0.03, 0.08 ± 0.04, 0.09 ± 0.05) respectively for wet rice during the WS, wet and dry rice during the DS across the sources over all growing stages. The results with prior information (SWC and RLD) (3rd row in Figs. 4, 5 and 6) showed heterogeneous distributions of soil water sources' relative contributions with the highest values at the surface (MFV 9–31%) and lowest at the lower soil depths (MFV ~3%) following the RLD and SWC distribution along the depths. The density distributions also were higher at the surface with the range of 0.72 ± 0.04, 0.67 ± 0.03, 0.61 ± 0.01 and decreases towards the end of the soil profile with the range of 0.28 ± 0.07, 0.30 ± 0.04, 0.30 ± 0.04 for wet rice during WS, wet and dry rice during DS respectively. The MFVs followed the same pattern, higher at the surface (0.65 ± 0.08, 0.59 ± 0.04, 0.24 ± 0.05) and decreased to the value of 0.003 at the end of the profile during all growing stages. During both WS and DS, SW was estimated to contribute the most to RWU (55–72%) of the wet rice plants. However, the ranges of contribution remained as high as when informative prior information were not included. Note that this was the case for all potential water sources.

During the WS, according to the informative prior observations the main plant water source was SW, with contributions of approximately 72, 56, and 68% during GS1, GS2, and GS3, respectively. During GS1, soil water at the surface (0–0.02 m) contributed about 14, 17, and 9% during GS1, GS2, and GS3, respectively. 3% of plant water uptake was located from 0.02 to 0.05 m during GS1. This proportion increased to approximately 18% during GS2 and then decreased to 7% during GS3. However, during GS2, plant roots reached down to 0.15 m, where they extracted about 10% water from 0.1 to 0.15 m soil depths. During the DS, throughout all growing stages, wet rice plants utilized mostly SW (56–63%), followed by surface soil (0–0.02 m) at 9–12%. The soil layers between 0.02 and 0.1 m contributed less (5%) during GS1 but increased to around 22% during GS3, when the plants extracted 5% of their water deeper in the soil profile (0.1–0.15 m). Dry rice took up 20–30% of its water from surface soil (0–0.02 m) and shallow soil water contributed to between 17 and 23%, 15 and 21%, and 5 and 13% to RWU at 0–0.05, 0.05–0.1, and 0.1–0.15 m soil depth, respectively, during the entire growing period. Dry rice plant roots reached down to depths of 0.15–0.3 m where they extracted 5–9% of their water, during GS3.

Discussion

Evaporation-affected isotopic compositions

The comparison between on the one hand the regression line onto which soil water samples fall in dual isotope ($\delta^{18}O$,$\delta^{2}H$) space and on the other hand the LMWL, enables identifying the prevailing conditions during fractionating evaporation in the different growing stages of wet and dry rice (Fig. 3). Since rainfall and soil textures were similar across sites, we concluded that

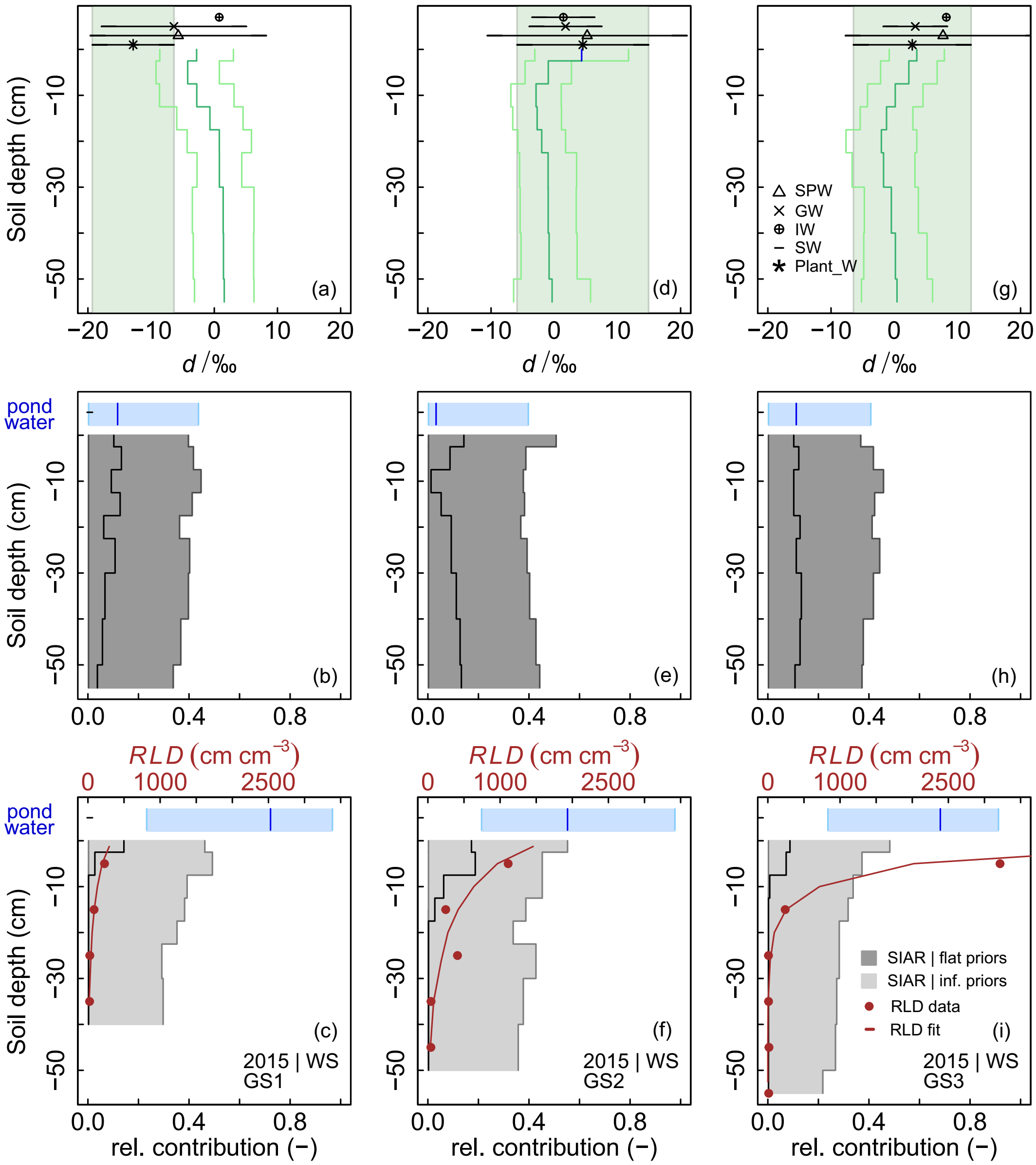

Fig. 4 Deuterium excess (d-excess) of soil water depth profiles (1st row; **a**, **d**, **g**; in green) where light-colored profiles indicate the boundaries of the 95% confidence interval (±1SD) together with d-excess of plant stem water, irrigation water (IW), ground water (GW), and surface ponded water (SW). Depth profiles of source's relative contribution to root water uptake with flat priors (2nd row; **b**, **e**, **h**) and informative priors (3rd row; **c**, **f**, **i**) GS1 (1st column; **a**–**c**), GS2 (2nd column; **d**–**f**), and GS3 (3rd column; **g**–**i**) refer to vegetative, reproductive, and ripening stages from wet rice during the wet season 2015

irrigation was the only external factor responsible for the slope differences. The decreasing slope (Table 2) with the drying of the soil can be explained by the increase in the effective thickness of the vapor transport layer (e.g., Barnes and Allison 1988). The isotopic kinetic effect was greater for soils (Cooper et al. 1991) under wet rice compared to dry rice soils as we observed higher slopes of the evaporation water lines under dry rice fields. The soil and plant water isotopic compositions from wet and dry rice during the DS were not significantly different (Fig. 3d–i). Deeper soil water derived from the GW and also from enriched recharged water and consequently, it reflected an enriched isotopic signal. Shallow soil water can be enriched due to evaporative isotope effects. Therefore, the isotopic compositions of soil water were higher than that of GW, and evaporation lines' slopes

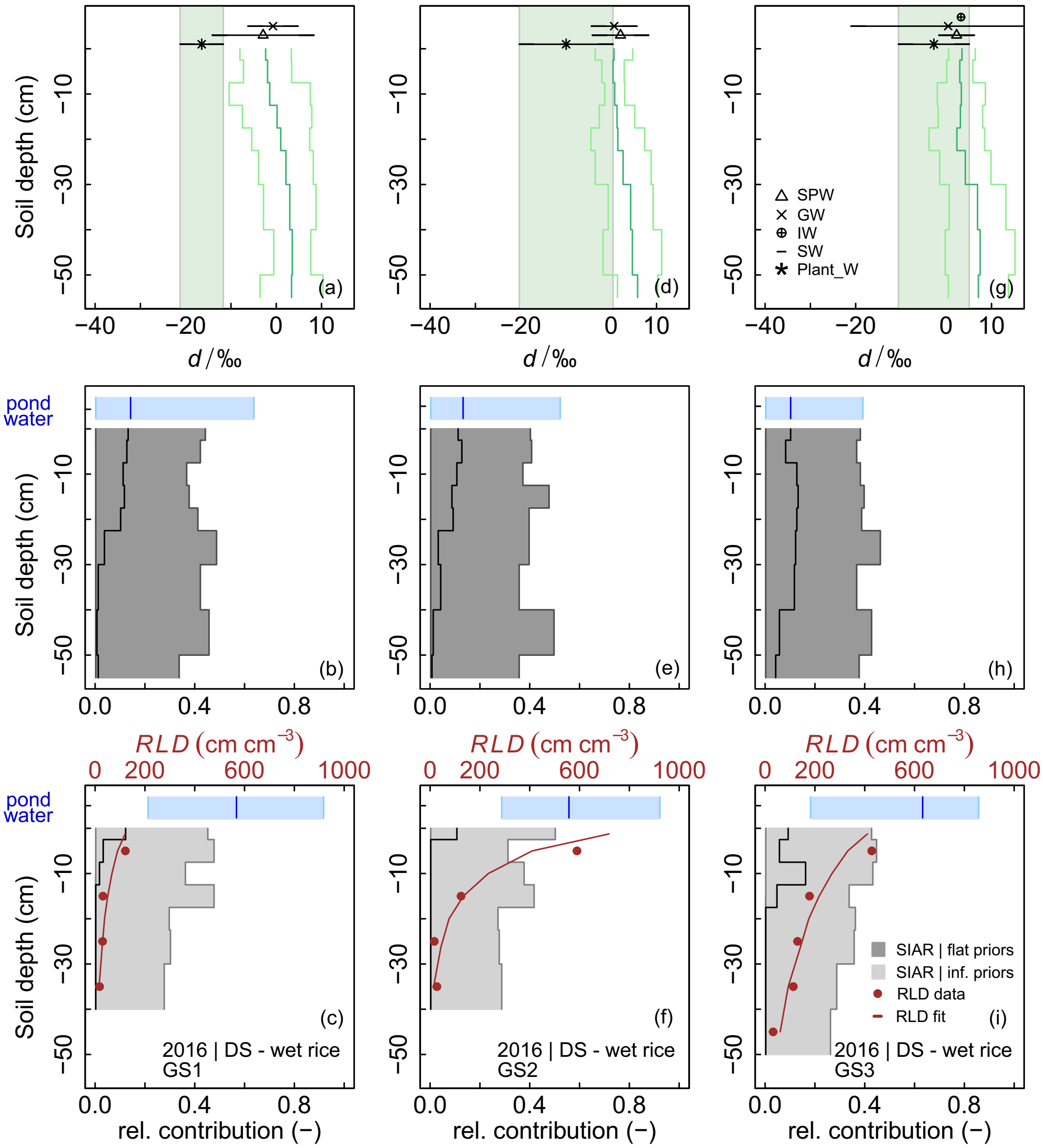

Fig. 5 Deuterium excess (d-excess) of soil water depth profiles (1st row; **a**, **d**, **g**; in green) where light-colored profiles indicate the boundaries of the 95% confidence interval (±1SD) together with d-excess of plant stem water, irrigation water (IW), ground water (GW), and surface ponded water (SW). Depth profiles of source's relative contribution to root water uptake with flat priors (2nd row; **b**, **e**, **h**) and informative priors (3rd row; **c**, **f**, **i**) GS1 (1st column; **a**–**c**), GS2 (2nd column; **d**–**f**), and GS3 (3rd column; **g**–**i**) refer to vegetative, reproductive, and ripening stages from wet rice during the dry season 2016

were lower for soil water than for SW or GW. Typical slopes of the regression lines would be about 5 for open water bodies, although the slope of evaporation varies with the humidity of the air (Darling 2004), where we observed ~6 for SW during both seasons.

Furthermore, GW was isotopically in a similar range with SW, but GW compositions were slightly lower compared to SW, which showed similar evaporation water line slopes (Fig. 3). This stemmed from the fact that the wet rice fields were abundantly irrigated (Fig. 1) and kept flooded with a high SW level for several weeks; the infiltration and percolation of SW to GW lead to a mixed water body (Sophocleous 2002). Allison et al. (1985) early observation on clustered data of GW isotopic compositions supported our finding of isotopically enriched

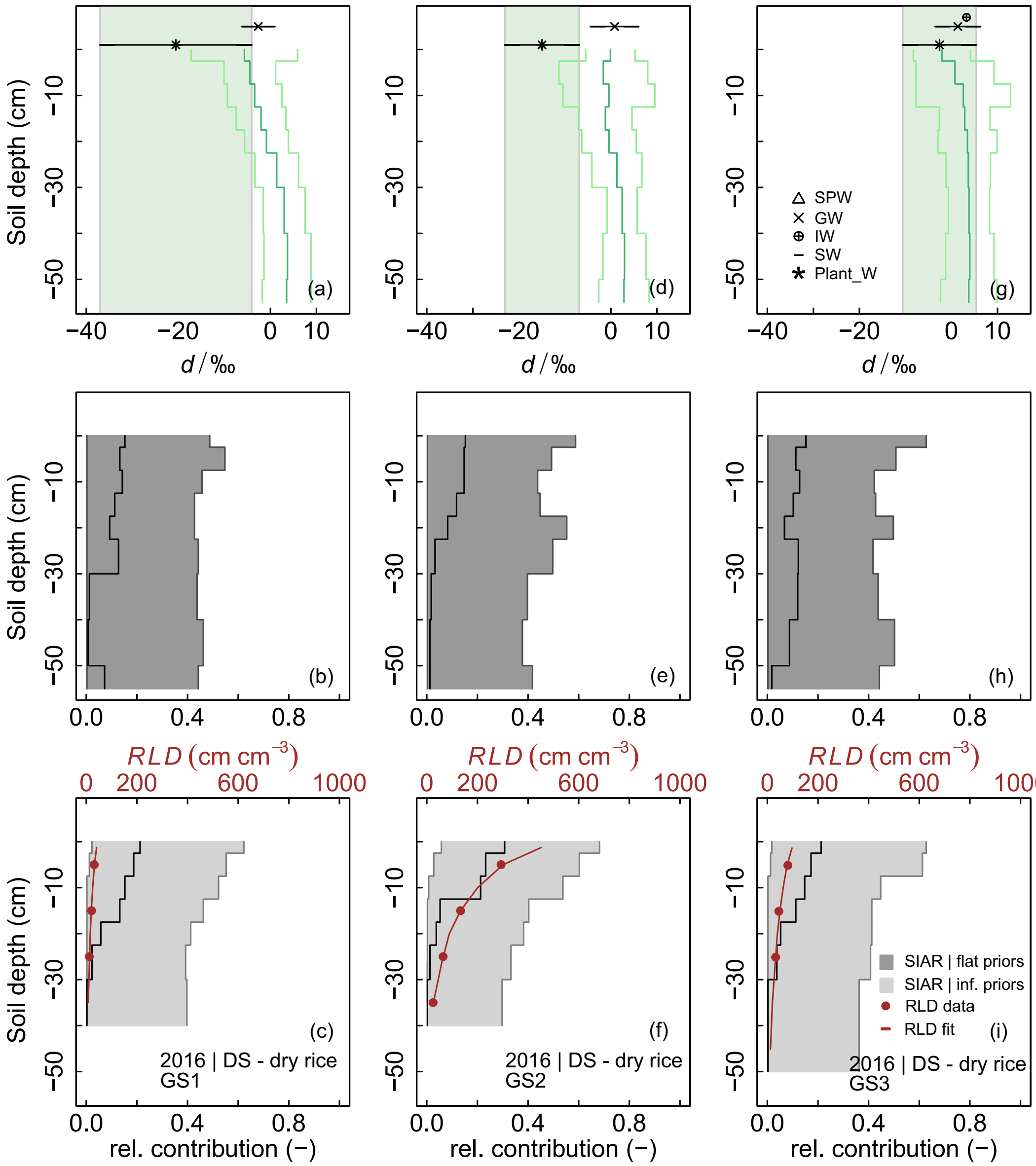

Fig. 6 Deuterium excess (d-excess) of soil water depth profiles (1st row; **a, d, g**; in green) where light-colored profiles indicate the boundaries of the 95% confidence interval (±1SD) together with d-excess of plant stem water, irrigation water (IW), ground water (GW), and surface ponded water (SW). Depth profiles of source's relative contribution to root water uptake with flat priors (2nd row; **b, e, h**) and informative priors (3rd row; **c, f, i**) GS1 (1st column; **a**–**c**), GS2 (2nd column; **d**–**f**), and GS3 (3rd column; **g**–**i**) refer to vegetative, reproductive, and ripening stages from dry rice during the dry season 2016

GW relative to the surrounding water pools. During the DS, the RW δ^2H and δ^{18}O compositions (8.1 ‰ and − 0.1 ‰, respectively) were higher than those during the WS, due to higher evaporative losses from small rain events. Because of reduced rainfall, soil water might have been a mixture of IW and upward fluxes of GW, which is common in arid and semiarid areas, as observed by Seyfried et al. (2005).

Potential methodological issues

Plant water isotopic enrichment was a notable issue in our study (Fig. 3) during early stages of rice growth. In this case, the plant xylem water isotopic composition does not reflect some mixture of the different contributing water sources (Thorburn and Ehleringer 1995; Dawson 1996). In our study, we observed, particularly during GS1 and GS2 in both seasons, that the plant water isotopic composition did not match with any of those of the soil water sources. Possible explanations for this was (i) stem evaporation from the rice plants (Helliker and Ehleringer 2002), (ii) back-diffusion of enriched leaf water during transpiration, or else (iii) diffusion of phloem enriched water into the xylem vessels (Cernusak et al. 2005; Bertrand et al. 2014). Martín-Gómez et al. (2017) stated that the major effect of stem transpiration on the isotopic composition of xylem water was due to limited leaf transpiration in early stages (Sperry et al. 1993). During our study, we avoided sampling green stem tissue; however, during early growing stages, the whole rice plant was generally small and green, which could have affected the isotopic results. Other explanations for these isotopic discrepancies could be isotopic fractionation (iv) during plant water uptake and/or (v) transport in the xylem vessels (Ellsworth and Williams 2007; Arnold et al. 2015; Vargas et al. 2017), and/or finally (vi) redistribution via diffusion or anabolic processes (Zhao et al. 2016). However, to our knowledge, issues (iv)-(vi) have not been observed and documented for rice plants. Another potential issue could have arisen from (vii) the clayey soil texture. The soil in our study has high percentages of vermiculite, smectite (as three layer clay), and some amount of kaolinite (as two layer clay). Gaj et al. (2017) stated that soil water extracted under vacuum displayed lower isotopic compositions due to different clay minerals and their strength of binding water. Therefore it is possible that water extracted under vacuum (i.e., bulk as well as tightly-bound water) was isotopically significantly different than plant xylem water since rice plants had generally easy access to bulk water (high soil water availability). Finally, errors during the extraction of water under vacuum should be accounted for (Orlowski et al. 2016); they were however not likely the major cause for differences between the source and plant water isotopic compositions in early stages, because all water extractions were performed with the same extraction line by the same operator. Additionally, in matured stages, the difference between plant and sources isotopic composition was not significant, which would support to dispose of the argument on the errors of the extraction method.

Where do rice plants take up water during different growing stages?

During both seasons, SW was the primary plant water source for wet rice during all growing stages. This is in contrast to findings by Shen et al. (2015), who observed that rice plants utilized water from shallow soil layers during continuously-flooded, alternative flooding and drying conditions. However, wet rice soil surface water (0–0.02 m) was the second contributing source to RWU in our study. During GS2 in the WS, the isotopically depleted plant stem water was primarily supplied by SW and soil water from a depth of 0.15 m, which can be explained by a rooting depth down to 0.3 m during this growing stage (Fig. 2). Interestingly, plants took up water directly from ponded water during GS3 (Fig. 3c). During this time, more rainfall occurred, and irrigation was paused from the last week of September; therefore, plants may have preferred readily available and accessible RW directly via shallow roots. Plants' rapid response to onset rains was remarkable, during the WS 2015. Rice roots may have developed a new set of feeding roots before the upper soil was fully wetted, displaying a quick water uptake pattern in response to rainfall. This can be explained by the characteristics of rice roots, such as shallow rooting, sensitive responses, and lateral root branching (Kato and Okami 2011). This also can be supported by the presence of high RLD at 0–0.1 m depths (>0.003 cm cm^{-3}) during this time (GS3). However, this case was unusual, and it heavily depends on the rain and irrigation events, together with the sampling schedule.

Wet rice water uptake during the DS was similar to plant's uptake during the WS, except during GS3, when the plant roots extracted water from 0.15 m, which can be explained by the different RLDs.

In dry rice, due to the unavailability of SW, extraction of shallow soil water (0–0.02 m) and deeper soil water by matured plants was comparable to maize's water uptake patterns studied by Zhang et al. (2011a); Kondo et al. (2000). Kondo et al. (2000) further observed that rice plants under mild water stress (which is more comparable to our dry rice cultivation) extracted soil water from 0 to 0.2 m, where we observed extraction between 0 and 0.3 m throughout the growing stages. These results demonstrate that rice plants use SW after transplanting and mainly take up water from shallow soil layers later. The possible reasons we could identify for our observations are the (i) rice root system, (ii) existence of the hardpan, and (iii) flood irrigation, which we will discuss in following sections.

The effect of the rice rooting system

Rice is often described as a shallow-rooted crop (Yoshida and Hasegawa 1982) and has previously been shown to prefer extracting water from shallow soil depth (Shen et al. 2015), which is also true for shrubs and grassy plants (Canadell et al. 1996). The RWU depth gradually increases with increasing crop age (Wang et al. 2010b) and is related to the characteristics of the plants' rooting system. Kondo et al. (2000) showed that RLD is an important factor in the water extraction by rice plants because relative water extraction from the soil layers is almost proportional to the vertical distribution of root length density. However, we observed higher RLD in the shallower soil under flooded conditions than under dry (aerobic) conditions (Fig. 2), which was also observed by Kato and Okami (2011). During the DS of our study, dry rice rooting systems developed similarly to the wet rice rooting systems, although the RLDs were comparatively less than for wet rice roots in WS. Nevertheless, we found deeper roots for wet rice than for dry rice in contrast to Shashidhar et al. (2012). This may be due to the connected subsurface system under flooded conditions. Therefore, the wet and dry soil conditions may not have been adequately separated at the subsurface level. A major fraction of the water and nutrients moving into the plant comes from shallow water sources (Pate and Jeschke 1993) especially from 0 to 0.05 m for rice (Shen et al. 2015) and 0.2–0.8 m for maize during its growth (Zhang et al. 2011a). In our study, the proportion of soil water used by plants generally increased with increasing RLD.

The effect of the hardpan

The formation of a hardpan, i.e., a dense layer of soil usually found below the uppermost topsoil layer, is well-known in rice paddy systems. This typically compacted layer results from repeated ploughing and forms at the interface of the puddled topsoil and the non-puddled subsoil (Chen and Liu 2002). In our study, this was between 0.01 and 0.15 m depth. Wetland varieties of rice are genetically shallow-rooted and also sensitive to extension (Kondo et al. 2000), which could be terminated by any reason, e.g., the resistance of hardpan near the soil surface as well as the anaerobic environment, which also impairs root growth with depth. This compacted layer can reduce percolation and inhibit root penetration (Bouman 2007).

The effect of flood irrigation

Under flooded conditions, our study shows that the proportion of soil water used by plants was higher when the SWC was higher. Similar results were observed for rice under flooded conditions (Shen et al. 2015) and also rice and maize under intermediate water supply (Kondo et al. 2000). A continuous flooding has been proved to be detrimental to rice root growth (Sahrawat 2000; Kato et al. 2009) as it presents an unfavorable physicochemical environment such as anaerobic conditions and toxic substances (e.g. Fe^{2+}, Mn^{2+}, organic acids) (Vizier 1989; Yang et al. 2004). Therefore, appropriate water management is vital to improve rice root growth in order to improve the plant water uptake.

Mixing model limitations and improvements

The method of direct graphical inference used in previous studies (Shen et al. 2015; Prechsl et al. 2015; Wang et al. 2017) could not be applied to our data when there was no overlap between the plant and soil water isotopic compositions (1st and 2nd rows in Appendix). A clearer solution could only be found for most of GS3 and GS1 in dry rice, where the isotopic composition of at least one water source intersected with that of the plant stem water (1st row in Figs. 4, 5 and 6). Following the recommendation of Rothfuss and Javaux (2017), multi-source mixing models should be preferred over the direct graphical inference method, because the latter simply ignores the possibility that plant water is a mixture of soil water from different layers. By using knowledge-based prior information, we quantified the SW and shallow soil surface water as active water sources. When the default flat priors were used, SIAR was not able to discern any particular trend in the RWU contributions of the different sources. On some occasions (e.g., GS2 during the WS and GS2 of dry rice during the DS), the simulated distribution of the most frequent values of the soil water sources' contributions followed the vertical distribution of the combined variable RLD*SWC (Eq. 2). This means that the root system extracted water proportionally to the RLD, which tends to occur when SWC is constant across all depths. To the contrary, a discrepancy between SIAR simulations with flat priors and with informative priors suggests the existence of a mechanism of RWU compensation (Heinen 2014; Rothfuss and Javaux 2017), i.e., plant roots adapt to the heterogeneous soil water availability and extract water from water limited soil areas with potentially low RLD (e.g., GS2 wet rice during the DS). On the other hand, ranges of contribution across soil water sources remained high, i.e., almost unchanged in comparison to when flat priors were used, which highlighted the uncertainty of the results. The uncertainty of the simulation runs remain high, because there were simply less water sources accounted for in the analyses.

Water productivity improvement via efficient irrigation system

Measured grain yields (reported at a standard water content of 140 g water kg^{-1} fresh weight in a 5 m^2 sampling area) were in average 4.50 t ha^{-1}, 5.34 t ha^{-1}, and 3.56 t ha^{-1} during the WS for wet rice, and during the DS for wet and dry rice, respectively. By taking into account the total amount of water inputs to both rice production systems, water productivities (g yield per kg of water input) for wet rice during the WS was 1.17 g kg^{-1}, and for wet and dry rice during the DS equal to 0.67 g kg^{-1} and 1.75 g kg^{-1}, respectively. According to our results, water productivity, particularly which of wet rice, could be further improved if the water ponding depth was reduced. Assuming that our fields were maintained at a constant 0.015 m water level instead of water table fluctuations due to irregular irrigation, we calculated the amount of excess water by determining the water level difference (measured water table [m] – 0.015 m) for each field. This difference was further multiplied by each field's area (m^2) and summed up to obtain the total excess water for each field. This resulted in a possible saving of approximately 30% irrigation water during the WS 2015 and of 44% during the DS 2016. This was comparable to intermittent irrigation, which can reduce IW use by 27–37% (Shi et al. 2002). This would have increased the water productivity for wet rice during the WS of 1.6 g kg^{-1} and during the DS of 0.97 g kg^{-1}.Therefore, properly managed water-saving irrigation systems increase water productivity and would improve the economic viability of the rice and decrease the above-described environmental issues. However, such a fine-tuning of the water management would need a careful monitoring and replenishment of irrigation water.

Conclusions

Our results provide valuable insight into water uptake patterns across rice based cropping systems by means of measured and simulated water stable isotopic compositions using a multi-source Bayesian mixing model. Including prior model information resulted in a clear improvement of the model compared to non-informative modeling. Plants mainly used SW and shallow soil water throughout the different growing stages, with a minor contribution from deeper soil layers.

We further found that rice plants extracted water proportionally to the RLD, which occurs primarily when the water content profile is constant across all depths. During the WS and DS, wet rice mostly took up SW (56–72%). Dry rice during the DS used water from shallow soil layers (40–50%), with a subsequently larger contribution of up to 35% from deeper soil horizons when the plants were mature. During the DS, the main water source for RWU was often based on irrigation while during the WS rainfall played an important role in plant water uptake. Having a better understanding of where rice plants take up their water, proper water-saving irrigation management systems can be developed. Future research using Bayesian mixing models for quantifying relative RWU profiles should incorporate prior information, such as root length density and soil water content profiles to better constrain the model.

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Appendix

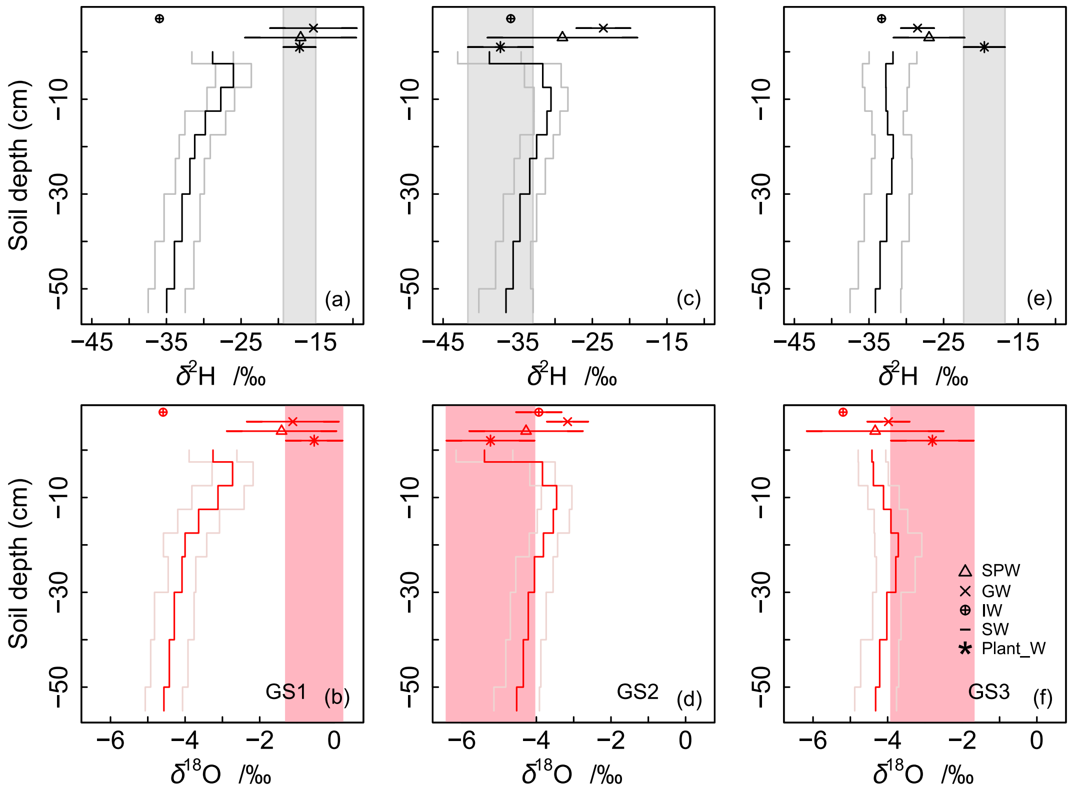

Fig. 7 Depth profiles of δ^2H (1st row; **a, c, e;** in black) and δ^{18}O (2nd row; **b, d, f**; in red) with corresponding plant stem water, irrigation water (IW), ground water (GW), and surface ponded water (SW) isotopic compositions with respective standard deviations. Light-colored profiles indicate the boundaries of the 95% confidence interval (±1SD). GS1 (1st column; **a, b**), GS2 (2nd column; **c, d**), and GS3 (3rd column; **e, f**) refer to vegetative, reproductive, and ripening stages from wet rice during the wet season 2015

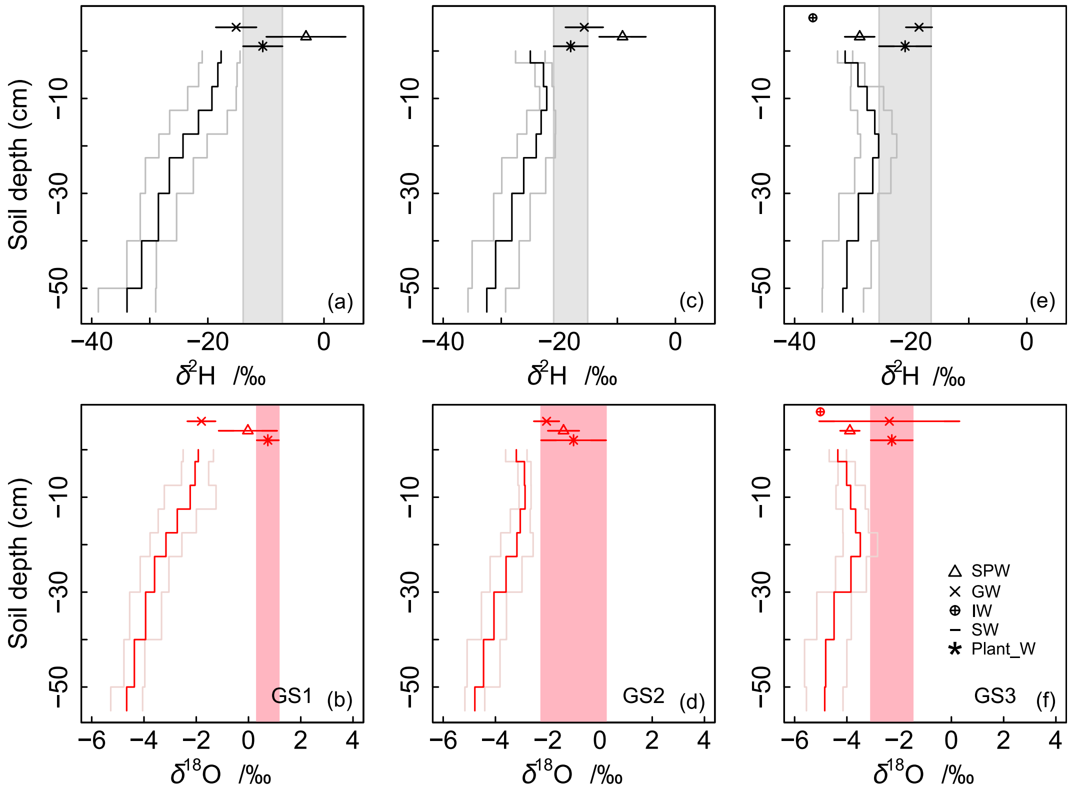

Fig. 8 Depth profiles of δ^2H (1st row; **a, c, e;** in black) and δ^{18}O (2nd row; **b, d, f**; in red) with corresponding plant stem water, irrigation water (IW), ground water (GW), and surface ponded water (SW) isotopic compositions with respective standard deviations. Light-colored profiles indicate the boundaries of the 95% confidence interval (±1SD). GS1 (1st column; **a, b**), GS2 (2nd column; **c, d**), and GS3 (3rd column; **e, f**) refer to vegetative, reproductive, and ripening stages from wet rice during the dry season 2016

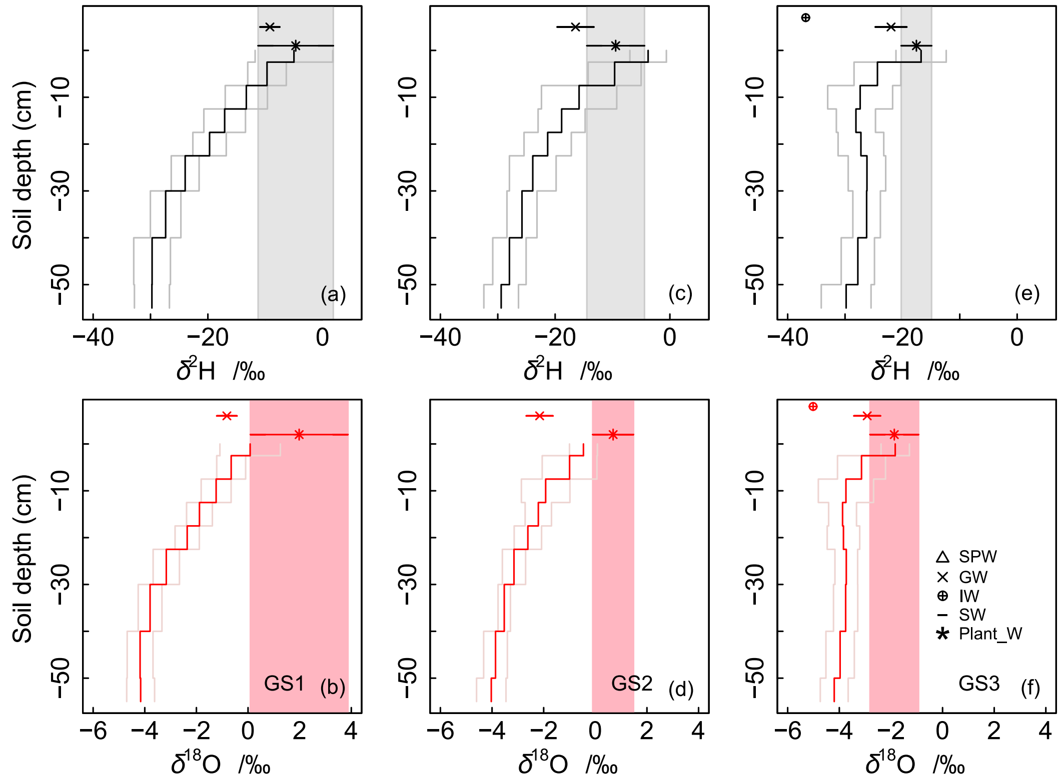

Fig. 9 Depth profiles of δ^2H (1st row; **a, c, e;** in black) and $\delta^{18}O$ (2nd row; **b, d, f**; in red) with corresponding plant stem water, irrigation water (IW), ground water (GW), and surface ponded water (SW) isotopic compositions with respective standard deviations. Light-colored profiles indicate the boundaries of the 95% confidence interval (±1SD). GS1 (1st column; **a, b**), GS2 (2nd column; **c, d**), and GS3 (3rd column; **e, f**) refer to vegetative, reproductive, and ripening stages from dry rice during the dry season 2016

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