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Stable water isotopes reveal modification of cereal water uptake strategies in agricultural co-cropping systems

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ABSTRACT

Agricultural co-cropping is being evaluated in temperate environments as a potential nature-based solution to the changing climate. However, the understanding of underlying physiological processes in co-cropping and its potential to provide climate resilience in temperate agroecosystems remains limited. This study investigated water sources for plants in five distinct cereal-legume co-cropping systems and four of their corresponding cereal monocultures at four main growth stages, under contrasting temperate hydro-climatological conditions in Scotland. Stable water isotope compositions (δ^2H and δ^{18}O) for soil water and xylem water were established. Based on the isotope compositions, a Bayesian multi-source mixing model was used to explore proportional soil water uptake patterns for cereal crop plants. Cereals grown in monocultures in this environment took more than 60 % of their water from the upper topsoil (soil depth <5 cm) during the main growth stages, under both wet and dry conditions. However, cereals cultivated as co-crops with legumes modified their water uptake strategy through increased water acquisition from the lower topsoil (5 – 30 cm) compared to monocultures, independent of environmental conditions. These novel findings suggest that co-cropping systems could potentially provide climate resilience for temperate agricultural systems. The findings provide an evidence-base for sustainable water planning, drought preparation and environmental intervention policies.

1. Introduction

Water for plants is often not limiting in humid temperate environments (Rodriguez-Iturbe et al., 2007). However, recent studies in the UK and other temperate zones found rising indications of water-stressed conditions in early spring and recurring drought conditions during summer (Blauhut et al., 2022; Fennell et al., 2020; Kleine et al., 2020). Future climate projections also highlight that these changes in climatic conditions will become more severe and widespread (Arnell et al., 2021; IPCC, 2023; Murphy et al., 2019). In Scotland, drought frequency is projected to at least double by 2050 affecting many economically important sectors, including the food and drinks industry (Visser-Quinn et al., 2021). Hotter and drier summers, as well as wetter autumn and winter seasons are predicted to cause water-stressed conditions and waterlogging, respectively, which could cause failure for cereal crops (Rivington et al., 2020).

To adapt arable farming to the threats of a changing climate, Nature-based solutions (NBS) and other innovative practices provide potential to help maintain crop productivity under limited resources (Anderson et al., 2020; Messean et al., 2021; Verret et al., 2020). One such practice is agricultural co-cropping (also referred to as intercropping) which involves the cultivation of two or more crop species or varieties simultaneously in the same field, either as row, strip, mixed or relay co-cropping (Stomph et al., 2020). While more common in arid, semi-arid and tropical climates, the practice of co-cropping is now also being evaluated in temperate agroecosystems as a viable NBS to address multiple challenges. These challenges include land nutrient deficiency (George et al., 2022; Rodriguez et al., 2021, 2020), increasing yield and land productivity (Weih et al., 2021), enhancing nitrogen (N) accumulation (Rodriguez et al., 2020), and promoting biodiversity (Brooker et al., 2015).

Co-cropping systems for efficient use of water and nutrient resources

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are broadly designed on two major principles; plant phenology and morphology traits (e.g., cereals - legumes, shallow - deep-rooted species), and resource complementarity traits (e.g., C3-C4 plants) (Gaudio et al., 2019; Stomph et al., 2020). While C3-C4 cereal-cereal and legume-legume combinations are common in non-temperate regions (Rodriguez et al., 2020), the most productive crop combinations in humid temperate regions usually involve C3-C3 cereal-legume combinations (George et al., 2022; Karley et al., 2018; Weih et al., 2021). In these systems, legumes are primarily used to reduce mineral fertiliser inputs to cereal crops (George et al., 2022; Rodriguez et al., 2020).

Plants can take up water from distinct or combinations of a range of sources such as from different soil depths, groundwater, or irrigation water when applied (Penna et al., 2020, 2018; von Freyberg et al., 2020). The proportional uptake of water from different sources can also vary through the growing season (Ma and Song, 2018). This can depend on changes in resource availability and crop water demand or the morphological structure of plant roots throughout the crop cycle (von Freyberg et al., 2020). However, it is also a factor of the modification ability (plasticity) of roots to changes in environmental conditions and resource availability (Jackson et al., 2000; von Freyberg et al., 2020). Some plants can also modify plant-water dynamics at small scale via excretion of mucilage, changing the soil and water dynamics in the rhizosphere (Marin et al., 2022). Interspecific relationships, that is, competition or complementarity in water use between plant species in co-cropping have been globally observed to vary depending on crop combination, soil hydrological conditions or growth stage (Chen et al., 2018; Hu et al., 2017; Yin et al., 2020). For example, maize (a cereal C4 plant) has been shown to exhibit plasticity in root architecture to increase water uptake from deeper soil sources when co-cropped with other species, hence saving irrigation needs and stabilising yields in non-temperate climates (Mao et al., 2012; Yin et al., 2020; Zhang et al., 2022). Here, a key question relates to evaluating crop combinations that can fulfil the principle of distinct resource complementarity traits (root and functional characteristics) in temperate regions for optimising water use. For instance, C4 and C3 crop combinations are found to be water efficient in arid, semi-arid and tropical climates (Li et al., 2020), but C4 plants are not common crop species grown in temperate climates (Sage et al., 1999). More investigation is also needed on the potential for co-cropping to promote ecological and environmental sustainability, specifically in the optimisation of soil water use (George et al., 2022).

Specifically, research in temperate regions has mainly focused on exploring above-ground processes in co-existing plants (Brooker et al., 2021; Homulle et al., 2021). The mechanisms of below-ground processes, such as soil water dynamics, water uptake patterns, and how this might change during the growing season under different soil hydrological conditions are largely unknown. The potential of co-cropping systems to improve agricultural production resilience to climate change, including drought and temperature rise in humid temperate agroecosystems, is yet to be fully understood or realised. Few existing studies conducted in temperate ecosystems were limited to water uptake within one growing season and showed variable responses of co-cropped cereals to drought (Schmutz and Schöb, 2023; Sun et al., 2022).

These physiological processes can be assessed with stable isotopes of water (δ^2H and δ^{18}O). Over the last decades, water stable isotopes have proven to be effective tracers in determining plant water uptake dynamics, especially in natural environments (Ehleringer and Dawson, 1992; Penna et al., 2018; Scandellari et al., 2024). Hereby, plant water uptake patterns can be inferred from the comparison of the value of isotopic composition representative of plant water uptake (that is, sap xylem water) and those of its sources that are located across the soil profile (that is, at different soil depths) (Ceperley et al., 2024; Rothfuss and Javaux, 2017). The use of water stable isotopes has already gained interest for studies on plant–soil interactions and plant water source partitioning in forests (e.g., Goldsmith et al., 2019; Ren et al., 2022). In relatively few cases, these environmental tracers have also been applied in agroforestry (involving woody plant species) and some agricultural research (Bachmann et al., 2015; Muñoz-Villers et al., 2020; Sohel et al., 2021). But generally, these tracers have not been fully explored in agroecosystems and co-cropping systems, despite their many potential uses in understanding root water uptake patterns of co-existing species (Penna et al., 2020).

This study aimed to determine water uptake patterns of different cereal crop species in humid temperate co-cropping systems and compare these patterns with their respective monocultures. Water stable isotopes were used to explore water uptake patterns for typical cereal-legume crop combinations in Scotland.

Specifically, the objectives of the study were to:

1. Examine the temporal dynamics of soil water stable isotopes under different cropping systems.
2. Identify the sources of cereal plant water uptake grown in monocultures at different growth stages and under varying hydroclimatological conditions.
3. Assess changes in water uptake patterns for cereal plants when co-cropped with legumes under these contrasting conditions.

Herewith, it was hypothesised that if there are niche differences in water uptake between cereals in humid temperate co-cropping and their monocultures, these differences might be less pronounced than in other climates where water is not a limiting factor for plant growth.

2. Materials and methods

2.1. Study site and experimental setup

The research site is Balruddery Farm (56.48°N, 3.11°W; 67 m – 163 m above sea level), near Dundee, Scotland, UK (Fig. 1). It is an arable research farm covering about 178 ha which belongs to The James Hutton Institute, Scotland, UK. The farm is situated in a temperate humid arable environment with a long-term average daily temperature of 8.6 °C, annual precipitation of 800 mm, and an average annual potential water deficit of 50 – 70 mm (Hawes et al., 2018). The soil at the site is mainly classified as clay loam to sandy loam in texture and the stone content ranges from 10 – 20 % (Brown et al., 2021; Hawes et al., 2018). Average soil bulk density of the site is 1.35 g/cm^3 (Brown et al., 2021). Depths of topsoil in the farm range from 25 cm to 40 cm (Hawes et al., 2018).

Two experimental field trials were conducted in two fields: field A (in 2022 and 2023 spring growing seasons) and field B (2023 spring growing season) (Fig. 1, S1). In fields A and B, the trial involved four and five cropping systems of monoculture or co-cropping, respectively (Table 1). These cropping systems consisted of four monocultures and five co-cropping of a cereal and a legume taken from three barley (*Hordeum vulgare*) cultivars with contrasting characteristics or one wheat (*Triticum aestivum*) cultivar, paired with two pea (*Pisum sativum*) cultivars, or one bean (*Phaseolus vulgaris*) cultivar or one faba bean (*Vicia faba*) cultivar sown in mixed arrangement (Table 1). Experimental plots (6.25 m × 1.5 m each) were allotted using a randomised block design, with five replicates (plots) per cropping system. Each trial was surrounded with a guard row of barley (Figure S1).

The cereal-legume crop combinations were selected based on different phenologies and morphologies. They have potential resource complementarity traits in terms of root characteristics (deep-rooted vs shallow-rooted), which is relevant for efficient water uptake with the assumption that these could result in some degree of complementarity (Stomph et al., 2020). Two cereal crops, spring barley and spring wheat were selected for the study. Spring barley is a dominant crop within the region, and important to the distillery and export economy of Scotland (Duffy et al., 2023) while spring wheat was selected to test its potential resilience in co-cropping systems. The leguminous crop species were pea, bean and faba bean, which are all used for animal feed in the area and could provide nitrogen fixation to increase plant nutrient

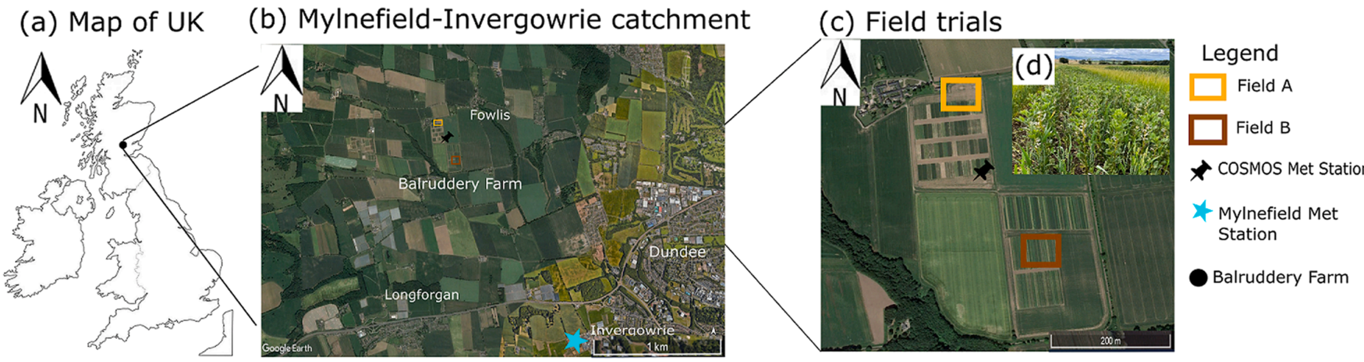

Fig. 1. The study location (a) Balruddery Farm in the North-East of Scotland, UK; (b) Mylnefield-Invergowrie catchment and surrounding area of Balruddery Farm with the location of Mylnefield (UK Met Office) Station; (c) The experimental fields with the location of COSMOS Met Station (where precipitation water sampler was installed for isotopes) (Source: Google Earth Pro); (d) Pictorial view of the cereals and legumes plants during the field trial.

availability.

The mix ratios of sowing densities (Table 1) were similar to that used in other trials involving the same crops (Karley et al., 2018; Pappagallo et al., 2021). A greater or similar proportion of cereal to legume was selected because cereal is the primary crop due to its significant economic value while legume is the secondary crop, providing soil nitrogen fixation. Throughout the growing seasons, there were no applications of pesticide, herbicide or irrigation in any of the fields.

2.2. *Field data collection and environmental conditions*

During the study period, climatic data and soil Volumetric Water Content (VWC) were continuously monitored at the COSMOS Met Station (56.482° N, 3.112° W; altitude 130 m; https://cosmos.ceh.ac.uk/), located approximately 320 m south of field A and 200 m northwest of field B (Fig. 1). Additional long-term (1960–2021) daily climatic data for the Mylnefield-Invergowrie catchment were obtained from the Mylnefield (UK Met Office) Station (56.456° N, 3.069° W; altitude 26 m), located about 5.1 km southeast of the research site. Overall, the first study year (October 2021-September 2022) was drier and warmer than the second (October 2022-September 2023) (Table S1). However, across both study years, similar temporal patterns were observed with daily mean air temperature steadily increasing from 5 °C in April to above 20 °C, before declining in August (Fig. 2). Daily potential evapotranspiration (PET) also followed a similar trend.

Soil VWC at the COSMOS station (hereafter referred to as COSMOS data) was obtained from cosmic ray neutron sensing data (Cooper et al., 2021; Smith et al., 2024). In addition, for the 2023 growing season in field A, daily soil VWC was continuously monitored in-situ in one plot (replicate) per cropping system (that is, 4 in total) using PR2 SDI-12 Soil Moisture Profile Probes (Delta-T Devices Limited, Cambridge, UK) recording at 10, 20, 30 and 40 cm soil depths (hereafter referred to as in-situ probes data). The in-situ probes showed similar temporal patterns to the COSMOS data. They also revealed that soil VWC generally increased with depth (that is, the deeper two depths, 30 and 40 cm, were mostly wetter or equal to the shallower layers, 10 and 20 cm) (Figure S2). However, it was not possible to distinguish differences between cropping systems, given the point scale heterogeneity in soil properties.

During the four intense sampling occasions (19 August 2022, 16 May 2023, 22 June 2023 and 18 July 2023) for water stable isotopes (see Section 2.3), soil VWC at 2, 5, 10, 20 and 30 cm soil depths were also determined using a SM300 time domain reflectometry (TDR) sensor (Delta-T Devices Limited, Cambridge, UK) (n = 9) (hereafter referred to as TDR data). The first sampling of soil and vegetation on 19 August 2022 followed a three-month dry spell with low soil VWC (COSMOS data) of < 25 % (Fig. 2, Table 2). On this day, average TDR soil VWC at the experimental plots increased from 18 % at 2 cm to 23 % at 30 cm depth. In comparison, the sampling on 16 May 2023 occurred when soil VWC (COSMOS data) was higher (Table 2). The TDR soil VWC measured at the experimental plots was 14 % at 2 cm depth and increased to 30 % at 30 cm. The sampling on 22 June 2023 occurred in the middle of a two-month dry spell when the soil VWC (COSMOS data) was consistently low (~22 %) with air temperature reaching 16.1℃ (Fig. 2). Soil VWC (TDR data) of 16 % was observed in the upper 20 cm depth and 11 % at 30 cm depth which was the lowest during the study. The sampling on 18 July 2023 was at a rewetting phase after the dry spell in June, with a monotonic soil VWC (TDR data) of 17 % from 2 – 30 cm depth.

The discrepancies between the COSMOS data and TDR VWC field measurements, with the latter generally lower, are due to differences in methods and topographical locations. COSMOS data provide information on general wetness in time and averaged over 15 cm depth, while TDR measures soil VWC at various depths. Topographically, the field

Table 1
Overview of the cropping systems grown during the spring crop cycle.

Field	Cropping systems	Shortened name	Sowing density (seeds m^{-2})	Mix ratio (%)	Crop cycles
A	Barley (*Hordeum vulgare* var. Laureate) Monoculture	*BL*	360	-	1. 18 April 2022
A	Barley (*Hordeum vulgare* var. Laureate) and Pea (*Pisum sativum* var. LG Stallion) Co-cropping	*BL&PS*	252 + 28.5	70 + 30	to
A	Barley (*Hordeum vulgare* var. KWS Sassy) Monoculture	*BS*	360	-	16 September 2022
A	Barley (*Hordeum vulgare* var. KWS Sassy) and Pea (*Pisum sativum* var. LG Stallion) Co-cropping	*BS&PS*	252 + 28.5	70 + 30	2. 27 March 2023 to 25 August 2023
B	Barley (*Hordeum vulgare* var. Bere) Monoculture	*BB*	816	-	1. 17 May 2023
B	Barley (*Hordeum vulgare* var. Bere) and Bean (*Phaseolus vulgaris* var. Scottish bean) Co-cropping	*BB&BE*	408 + 42.6	50 + 50	to
B	Wheat (*Triticum aestivum* var. WPB Escape) Monoculture	*W*	100	-	26 September
B	Wheat (*Triticum aestivum* var. WPB Escape) and Faba bean (*Vicia faba var.* Yukon) Co-cropping	*W&FB*	90 + 49.5	90 + 90	2023
B	Wheat (*Triticum aestivum* var. WPB Escape) and Pea (*Pisum sativum* var. Orchestra) Co-cropping	*W&PO*	80 + 80	80 + 100	

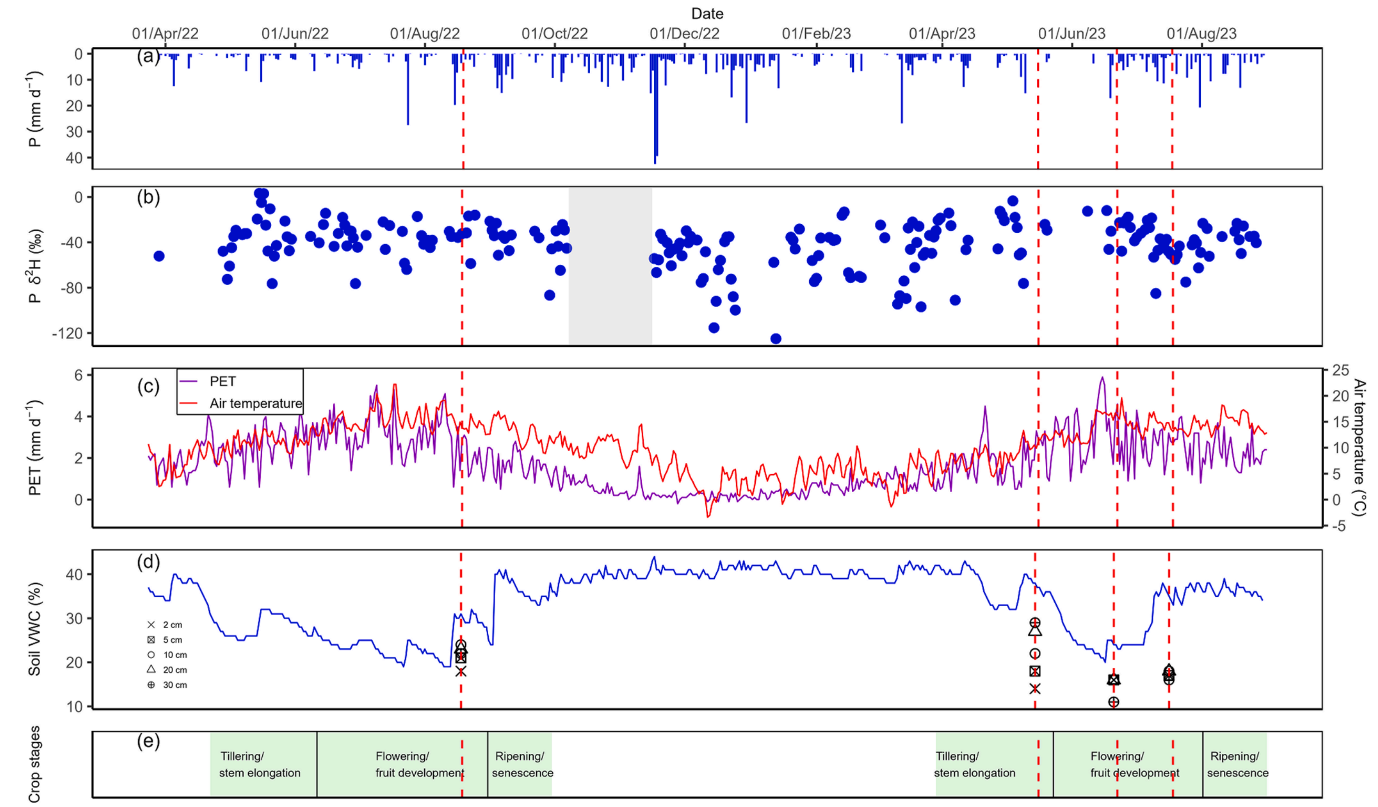

Fig. 2. Hydro-climatological data during the study period. (a) Daily Precipitation amount (P, mm d^{-1}) and (b) Hydrogen isotope composition (δ^{2}H, ‰). The grey shaded band represents a period of missing data due to a faulty apparatus; (c) Daily air temperature and Potential Evapotranspiration (PET) calculated using weather station data and the Penman-Monteith equation; (d) Blue line represents daily soil Volumetric Water Content (VWC) for the upper ~15 cm soil depth measured at the COSMOS Met Station. Unique symbols show average values of soil VWC (TDR data) measured at different depths during the sampling occasions in the experimental field; (e) Phenological crop growth stages. The green bands represent the periods of each growth stage. The red dash lines represent the plants and soil sampling occasions for isotope analysis.

Table 2
Summary of environmental conditions during the sampling occasions.

Parameters	19 Aug 2022	16 May 2023	22 Jun 2023	18 Jul 2023
Antecedent precipitation (mm) *[Sum of P for 7 days before sampling]*	35	15	22	27
Air temperature (°C)	13.8	11.3	16.1	13.1
PET (mm)	2.9	2.9	4.6	2.7
Weather station (COSMOS) soil VWC (%) *[Averaged upper 15 cm]*	30	38	24	35

site is at the top of the hill, whereas the COSMOS station is at the bottom.

2.3. Water stable isotope sampling procedures

2.3.1. Precipitation

To understand temporal hydro-climatological processes for reference, daily precipitation was sampled for isotopic analysis (δ^{2}H and δ^{18}O) at 24-hour temporal resolution with an automatic water sampler (Teledyne ISCO 3700 Portable Water Autosampler) installed at the field site. A thin layer ~1.5 cm of paraffin oil was added to the storage bottles prior to sample collection to prevent evaporative fractionation. At least once every ten days, the storage bottles were emptied from the automatic sampler then replaced with cleaned bottles. The collected samples were stored in the fridge (at 4°C) prior to isotopic analyses.

2.3.2. Water in soil and plant xylem

Soil and cereal plant xylem samples were collected from all the cropping systems at different stages of the crop cycle for determination of water δ^{2}H and δ^{18}O following the guidelines described by Ceperley et al. (2024). These growth stages included the late seed development, stem elongation, flowering and early seed development on 19 Aug 2022 (field A), 16 May 2023 (field A), 22 June 2023 (fields A & B) and 18 July 2023 (fields A & B), respectively. These dates corresponded to dry, wet, very dry and rewetting soil hydrological conditions, respectively (Fig. 2) (see Section 2.2). Each sampling date was preceded by three or more days with no rain, to avoid contamination by wet vegetation.

Soil samples (~ 10 g each) were collected from each cropping system plot using an auger in 5 different layers (0–2 cm, 2–5 cm, 5–10 cm, 10–20 cm, and 20–30 cm) within the rooting depth. The rooting depth and associated water uptake for the study plant species in this type of environment is relatively shallow, with turnover and production of fine roots known to be typically in the top 20 – 30 cm of the soil profile (Amin et al., 2020; Fan et al., 2016; Geris et al., 2017).

At the same time, samples (~ 5 g) of the cereal crop species were destructively taken from the root crown, which is known to best match plant source water under the assumption that there is no evaporative fractionation (Barnard et al., 2006). The epidermis of the root crowns were carefully removed using tweezers and cleaned to remove soil. For each cropping system, four individual plant tillers were collected and pooled together in each of three glass vials. The twelve individual plants were randomly selected to cover the natural observed spatial heterogeneity at each development stage.

All soil and plant samples were stored in 12 mL air-tight glass exetainers (Labco Limited, UK) and double-sealed with Parafilm®. A maximum of approximately 1 cm headspace was allowed in the exetainers to limit eventual isotopic effects resulting from water vapor exchange with ambient air during transport and storage in the fridge (at

4°C) prior to extraction in the laboratory.

2.3.3. Cryogenic vacuum distillation of soil water and plant xylem water

Water from the soil and plant samples was extracted by cryogenic vacuum distillation (CVD) (Orlowski et al., 2013) at the water isotope laboratory of the Institute for Bio- and Geosciences, Agrosphere (IBG-3) (Forschungszentrum Jülich, Germany). Extraction was done at working pressures ranging between 2.0 x 10^{-3} and 1.0 × 10^{-2} mbar and at temperatures > 90 °C for about 3 – 4 h depending on the sample initial volumetric water content.

Potential impurities and organic contaminations were removed from the extracted water using 0.22 µm organic phase pin-type filters. Samples were transferred to 2 mL air-tight glass vials, sealed with Parafilm®, and stored in the fridge at 4°C prior to isotopic analysis. To evaluate the extraction efficiency, the weights of the initial plant and soil samples were sequentially compared prior to extraction, immediately after extraction, and after drying the extracted samples at 105°C for 24 hours. The extraction efficiency was > 98 % as recommended by Ceperley et al. (2024).

2.4. Water isotope analyses

Precipitation samples were analysed at the University of Aberdeen for δ^2H and δ^{18}O using a triple water-vapour isotope analyser (off-axis integrated cavity output spectroscopy [OA-ICOS], TWIA-45-EP, Model: 912–0032–0000, Serial:14–0038) with a long-term precision of 0.4 ‰ for δ^2H and 0.1 ‰ for δ^{18}O. Soil and plant water δ^2H and δ^{18}O were determined at the Institute for Bio- and Geosciences, Agrosphere (IBG-3) (Forschungszentrum Jülich, Germany) using a Picarro L2130-i laser spectrometer (Picarro Inc., Santa Clara, CA, USA, precision of 0.5 ‰ for δ^2H and 0.1 ‰ for δ^{18}O.

All δ^2H and δ^{18}O isotopic values are reported in δ-notation which represents ‰ compositions relative to the Vienna Standard Mean Ocean Water Standard (VSMOW) expressed in permil (‰). Deuterium excess (d-excess), a measure to evaluate the impacts of isotope fractionation in soil water and plant xylem water due to evaporation effects (Dansgaard, 1964), was determined for all soil and plant samples following Eq. 1:

$$\text{d-excess} = \delta^2\text{H} - 8 \times \delta^{18}\text{O} \tag{1}$$

2.5. Statistical analyses of soil and plant samples

One-way MANOVA tests were conducted to evaluate differences between δ^2H and δ^{18}O values of different soil layers and of plant samples between cropping systems for each sampling occasion. Two-way MANOVA tests, each followed by a post-hoc Tukey's test, were used to evaluate differences in time. MANOVA tests were used since the isotope data from water samples meet the assumptions of normality and homogeneity of variance-covariance. All the statistical analyses were performed in R (v4.2.2) (R Core Team, 2022).

2.6. Bayesian end-member mixing modelling for plant water uptake

The likely proportional contributions to plant water uptake from distinct soil layers were determined using MixSIAR, a Bayesian end-member mixing model (Stock et al., 2018), available in R (v4.2.2) packages "MixSIAR" and "JAGS" (R Core Team, 2022). Only soil water was considered as the source for plant water uptake to reduce uncertainties and improve the model inference (Parnell et al., 2010; Stock et al., 2018; Stock and Semmens, 2016). Soil depths were aggregated into two end-members, namely, upper (<5 cm) and lower (5 –30 cm) topsoil layers for further analyses. For each cropping system, the δ^2H and δ^{18}O compositions of the soil profiles were similar and therefore pooled for each sampling occasion. There was an exception for July 2023, where the soil depths of each cropping system were aggregated differently and individually as appropriate to form distinct end-members, mostly three (Figure S3). This was needed because the samples of the July 2023 rewetting period were more heterogeneous across the cropping systems. However, to ensure comparison of results among all the sampling occasions, the end-member mixing results were presented for the proportional uptake from the upper topsoil (sum of 0–2 and 2–5 cm soil depths) and lower topsoil (sum of 5–10, 10–20, and 20–30 cm soil depths) for all the sampling occasions.

The four sampling occasions were modelled separately to evaluate any temporal changes in the patterns of the source proportional contributions. All individual soil water measurements of δ^2H and δ^{18}O from the distinct end-members were provided as model inputs with the corresponding individual cereal xylem δ^2H and δ^{18}O measurements. The soil isotopic data were weighted using the soil water content of each soil layer following Rothfuss and Javaux (2017). This approach was selected due to its incorporation of covariance between tracers to make a complete "fully Bayesian" model as opposed to solely introducing overall summary statistics, such as mean, standard deviation and sample size (Stock et al., 2018). While this ensures the model fully considers the complexity and interdependencies within the dataset, it was found that overall results were similar with and without the weighting of soil isotopic data. Based on the assumption that plant water uptake is not influenced by isotope fractionation, the discrimination factors of both δ^2H and δ^{18}O were set to zero (Ehleringer and Dawson, 1992; Rothfuss and Javaux, 2017; von Freyberg et al., 2020).

The individual models were set as "long" runs in MixSIAR, which consisted of three Markov chain Monte Carlo Bayesian models with 100 thins, 200,000 burn-ins and a chain length of 300,000 iterations to estimate the posterior distribution for each cereal plant water mixture. Both error options of "residual" and "process" were specified in the model. The outputs of each of the model runs were then approved using the Gelman-Rubin and Geweke diagnostic procedures to assess Markov chain Monte Carlo convergence (Gelman et al., 2013).

3. Results

3.1. Stable isotopic compositions of waters

3.1.1. Precipitation

The local meteoric water line (LMWL) was fitted to the daily precipitation samples data collected during the study at the research site as $\delta^2\text{H} = 7.1 \times \delta^{18}\text{O} + 2.7$ ($R^2 = 0.95$; $p < 0.001$). Isotopic composition of precipitation showed a strong daily variability and seasonality with summer precipitations most enriched while winter precipitations were most depleted (Fig. 2, showing δ^2H data only). The isotopic values of

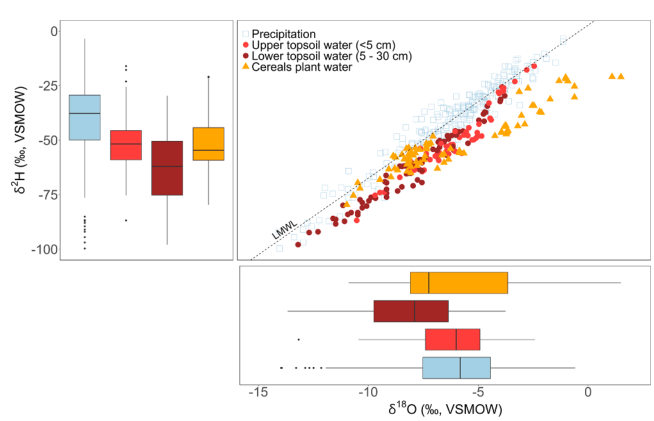

Fig. 3. Isotope composition of daily precipitation, upper topsoil water (< 5 cm), lower topsoil water (5 – 30 cm), and cereal xylem water pooled for all the sampling occasions. Additional box plots depict the range of the datasets. LMWL = Local meteoric water line.

Table 3
Mean ± (SD) δ^2H and $\delta^{18}O$ of precipitation, xylem water and bulk soil water, and equivalent deuterium-excess (d-excess) values (‰) for each sampling occasion.

Parameters		19 Aug 2022	16 May 2023	22 Jun 2023	18 Jul 2023
Precipitation	δ^2H (‰)	−27.1	−75.7	−42.2	−43.1
[weighted P for 7 days before sampling]	$\delta^{18}O$ (‰)	−4.5	−10.6	−6.4	−6.1
	d-excess	8.9	9.1	9.0	5.7
		n = 8	n = 8	n = 18	n = 18
Upper topsoil water (<5 cm)	δ^2H (‰)	−25.3 ± 4.8	−46.6 ± 3.5	−54.4 ± 5.8	−65.0 ± 12.9
	$\delta^{18}O$ (‰)	−3.6 ± 0.6	−5.0 ± 0.4	−6.3 ± 0.9	−8.3 ± 1.6
	d-excess	3.8 ± 0.8	−6.7 ± 2.5	−4.0 ± 3.0	1.1 ± 4.1
		n = 12	n = 12	n = 27	n = 27
Lower topsoil water	δ^2H (‰)	−41.3 ± 7.4	−55.8 ± 4.5	−78.2 ± 10.9	−67.5 ± 15.5
(5 – 30 cm)	$\delta^{18}O$ (‰)	−5.3 ± 1.0	−6.9 ± 0.8	−9.9 ± 1.7	−8.6 ± 2.2
	d-excess	0.9 ± 1.4	−0.8 ± 3.6	0.7 ± 4.1	1.7 ± 4.1
		n = 12	n = 12	n = 27	n = 27
Cereal plant	δ^2H (‰)	−25.7 ± 4.9	−41.9 ± 4.5	−57.9 ± 5.1	−58.9 ± 7.7
Xylem	$\delta^{18}O$ (‰)	−1.0 ± 1.3	−3.2 ± 0.6	−7.0 ± 1.5	−8.3 ± 1.0
	d-excess	−17.5 ± 8.7	−16.4 ± 2.1	−1.7 ± 7.9	7.4 ± 2.8

precipitation ranged from −124.9 ‰ to 3.2 ‰ for δ^2H and from −14.0 ‰ to 0.6 ‰ for $\delta^{18}O$ (Fig. 3), with weighted averages of −45.9 ‰ and −6.8 ‰, respectively. The average δ^2H and $\delta^{18}O$ of the first study year were −36.2 ‰ and −5.3 ‰, respectively and were slightly higher than those of the second, −44.8 ‰ and −6.8 ‰, respectively. In terms of the sampling occasions, the weighted isotopic composition values of precipitation for the seven days preceding sampling was found to be most enriched for the August dry sampling (-27.1 ‰ for δ^2H; −4.5 ‰ for $\delta^{18}O$) while the most important depletion was in the May wet sampling (-75.7 ‰ for δ^2H; −10.6 ‰ for $\delta^{18}O$) (Table 3).

3.1.2. Soil water

The soil water δ^2H and $\delta^{18}O$ overlapped with precipitation isotopic composition values and plotted very close the LMWL, indicating that there was no substantial evaporative fractionation (Fig. 3). The soil water isotopic data ranged from −105.1 ‰ to −16.0 ‰ for δ^2H, and from −13.7 ‰ to −2.4 ‰ for $\delta^{18}O$. The data in Fig. 3 show that the upper topsoil water (<5 cm) was significantly more enriched in both δ^2H and $\delta^{18}O$ ($p < 0.05$) than the lower topsoil water (5–30 cm), except during the July 2023 rewetting period (Fig. 4; Table S2). Overall, there were significant variations in the average soil water δ^2H and $\delta^{18}O$ values with time, which reflected the variations in precipitation inputs (Table S2). There were no variations in soil water stable isotopes among the cropping systems except in July 2023 sampling when the widest range of variation was observed (Fig. 5). The June 2023 very dry period showed the most pronounced depletion in soil water δ^2H and $\delta^{18}O$ along the soil profiles.

3.1.3. Plant xylem water

The plant xylem water isotopic composition values for cereal crop species ranged from −79.6 ‰ to −20.9 ‰ for δ^2H, and from −10.7 ‰ to 1.5 ‰ for $\delta^{18}O$ (Fig. 3; Table 3). They mostly plot below the LMWL and largely overlapped with the soil water and precipitation values during all the samplings, indicating mixtures of the soil water with no substantial evaporative fractionation.

There were significant differences ($p < 0.05$) between the isotopic values of the cereals when grown in monocultures versus co-cropping for most cropping systems (Table S3) with some exceptions. The exceptions are barley co-cropping with pea during August (dry), barley (KWS Sassy) co-cropping with pea during May (wet), barley co-cropping with pea during June (very dry), and barley co-cropping with pea and bean during July (rewetting periods).

3.2. Modelled proportional contributions of soil water to cereal water uptake in monocultures

Cereals in all monocultures extracted ~ 60 % or more water from the upper topsoil (<5 cm), regardless of growth stage and hydro-climatological conditions (Fig. 6). There was a gradual but small increase in the proportion of lower topsoil (5 – 30 cm) water uptake as plant growth advanced. For example, during the May 2023 sampling, which coincided with the stem elongation stage, approximately 70 % of water in barley Laureate (*BL*) and barley KWS Sassy (BS) monocultures was taken from the upper topsoil. As plant growth advanced, this decreased to about 60 % during the late seed development stage (represented by the August 2022 sampling). Similarly, barley Bere (*BB*) and wheat (*W*) monocultures revealed decreases in soil water contributions from the upper topsoil between the flowering (June 2023) and early seed development growth stages (July 2023). However, hydro-climatological conditions also changed across the four time periods. It is worth noting that during the driest conditions (June 2023), the proportional uptake from the upper topsoil was highest for cereals in all the monocultures.

3.3. Modelled proportional contributions of soil water to cereal water uptake in co-cropping compared to when grown in monocultures

Generally, the co-cropped cereals used proportionally more of the lower topsoil water than when grown in monocultures during different environmental conditions (Fig. 7). Overall, the cereals in co-cropping also adjusted more to increasingly drier soil conditions by increasing lower topsoil water uptake more than their respective monocultures (Fig. 7). The exception is wheat which, when co-cropped with peas, consistently depended on upper topsoil water irrespective of growth stages or water availability condition. Also, barley KWS Sassy co-cropped with pea (*BS&PS*) exhibited the highest proportion of root water uptake from the lower topsoil compared with other co-cropping systems, especially during the July rewetting sampling. Furthermore, the water uptake patterns of the barley cultivars were not affected when co-cropped with either pea or bean. In contrast, wheat responded differently in water uptake when co-cropped with faba bean compared with when co-cropped with pea.

4. Discussion

This study revealed that cereals grown here in a temperate humid region mostly took up their water from the upper topsoil. Cereal crop water uptake patterns was also found to change when grown in cereal-legume co-cropping systems compared to cereals in monocultures, with a shift towards relatively more uptake from the lower topsoil water during critical growth stages. The following discussion will elaborate on these key findings, examining the spatio-temporal dynamics of plant water uptake, physiological mechanisms underlying the observed shifts, and the broader implications for sustainable agriculture and water resource management under a changing climate.

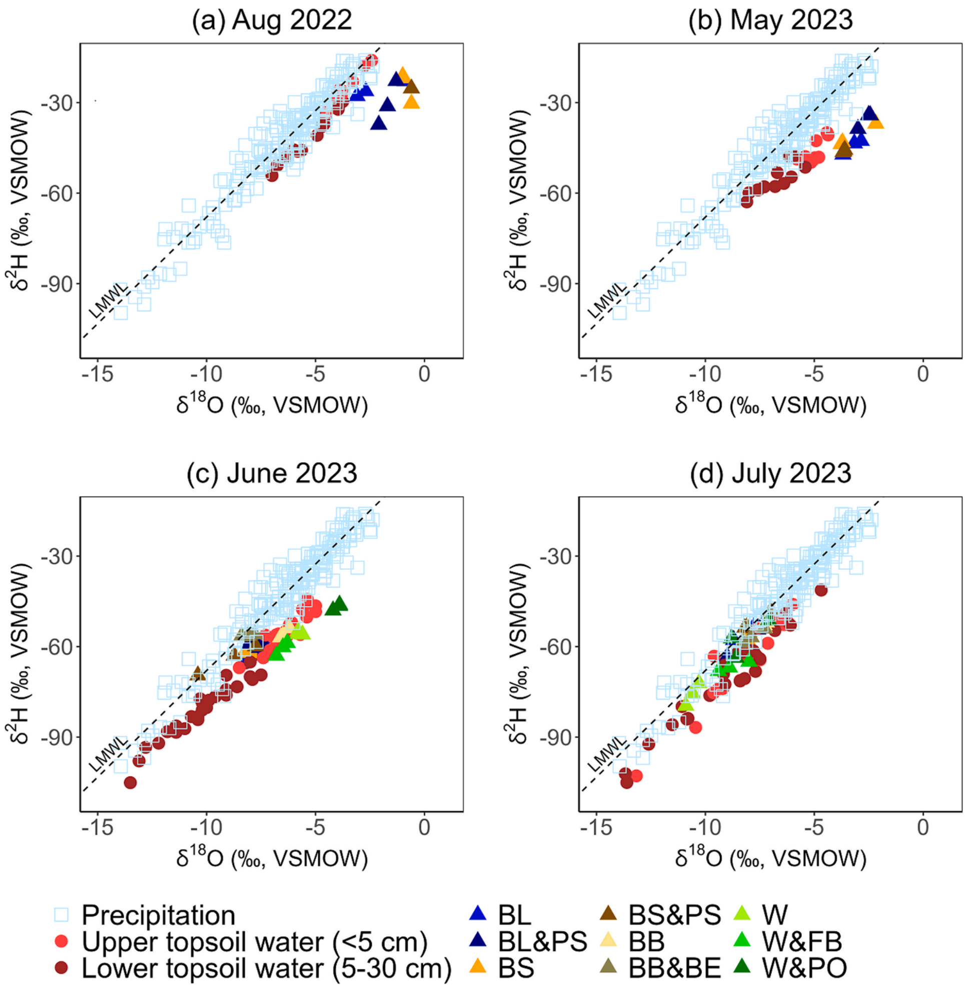

Fig. 4. Isotope composition of daily precipitation, upper topsoil water (< 5 cm), lower topsoil water (5 – 30 cm), and cereal xylem water per cropping system for each sampling occasion. LMWL = Local meteoric water line; *BL* = Barley (Laureate) monoculture; *BL&PS* = Barley (Laureate) co-cropped with pea; *BS* = Barley (KWS Sassy) monoculture; *BS&PS* = Barley (KWS Sassy) co-cropping with pea; *BB* = Barley (Bere) monoculture; *BB&BE* = Barley (Bere) co-cropped with bean; *W* = Wheat monoculture; *W&FB* = Wheat co-cropped with faba bean; *W&PO* = Wheat co-cropped with pea.

4.1. Spatio-temporal patterns in plant water uptake of cereals in monoculture

The upper topsoil water (up to 5 cm) was the most important water source for the cereals investigated. This is very different from main water uptake sources in arid and semi-arid regions where this has been reported to be between 20 – 70 cm soil depth (Ma and Song, 2018; Wu et al., 2018). It also contrasts with studies for cereals in other temperate, but higher energy, climates. For example, at research sites near Zurich in Switzerland, Schmutz and Schöb (2023) and Sun et al. (2022) reported 15–20 cm as the main water uptake source. This contradiction between the findings of this study with those in other temperate climates could be due to environmental differences. The site of this study is colder and wetter, with relatively lower energy and evapotranspiration. For example, the Balruddery Farm long-term average temperature during May-June is 10.2–13.1°C, compared with 13.9–17.2°C at the site of Sun et al. (2022) and 11.2–19.8°C at the site of Schmutz and Schöb (2023). Also, the soils remained relatively wet throughout. The lowest soil VWC observed here in the upper 15 cm was 22 % (as observed from the COSMOS data). This was not close to the permanent wilting point (11–15 %) as observed in the upper 20 cm soil depth at a nearby site with a similar soil type (Marin et al., 2022). It therefore suggests that the water stress was only ever 'moderate' at our study site and period.

The finding that the source of water uptake in cereals is near the soil surface is, however, consistent with previous studies on perennial species in northern cold environments. For example, Geris et al. (2015), (2017) and Tetzlaff et al. (2021) also found that the soil water source of woody tree and shrub species such as Scots Pine and heather was relatively shallow. The shallow soil water source of plants might also be related to nutrient availability and uptake (Andresen et al., 2016; Querejeta et al., 2021), thus raising more questions on how water and other nutrient uptake patterns might be correlated in this environment. This further emphasises the importance of considering differences in soil-plant interactions between climates since climate greatly influences soil composition and moisture levels (Seneviratne et al., 2010), affecting nutrient availability and plant growth.

Within the different monoculture systems, there were also changes in the proportional water uptake patterns under varying hydro-climatological conditions, and as plant growth advanced. This is similar to previous findings that cereal plants take up water from shallow sources where water is usually available as they grow, generally increasing uptake from other soil sources when topsoil water becomes limited but reverting back to shallow sources towards senescence (Ma and Song, 2018; Wang et al., 2010; Wu et al., 2018).

However, there was proportionally most water uptake from the upper topsoil during the very dry condition (June). This may be counterintuitive, but it is consistent with other studies where monoculture cereals (barley, maize and common millet) and legumes (cowpea and soybean) (Zegada-Lizarazu and Iijima, 2004) consistently relied on or shifted to shallower water sources instead of deeper and wetter depths

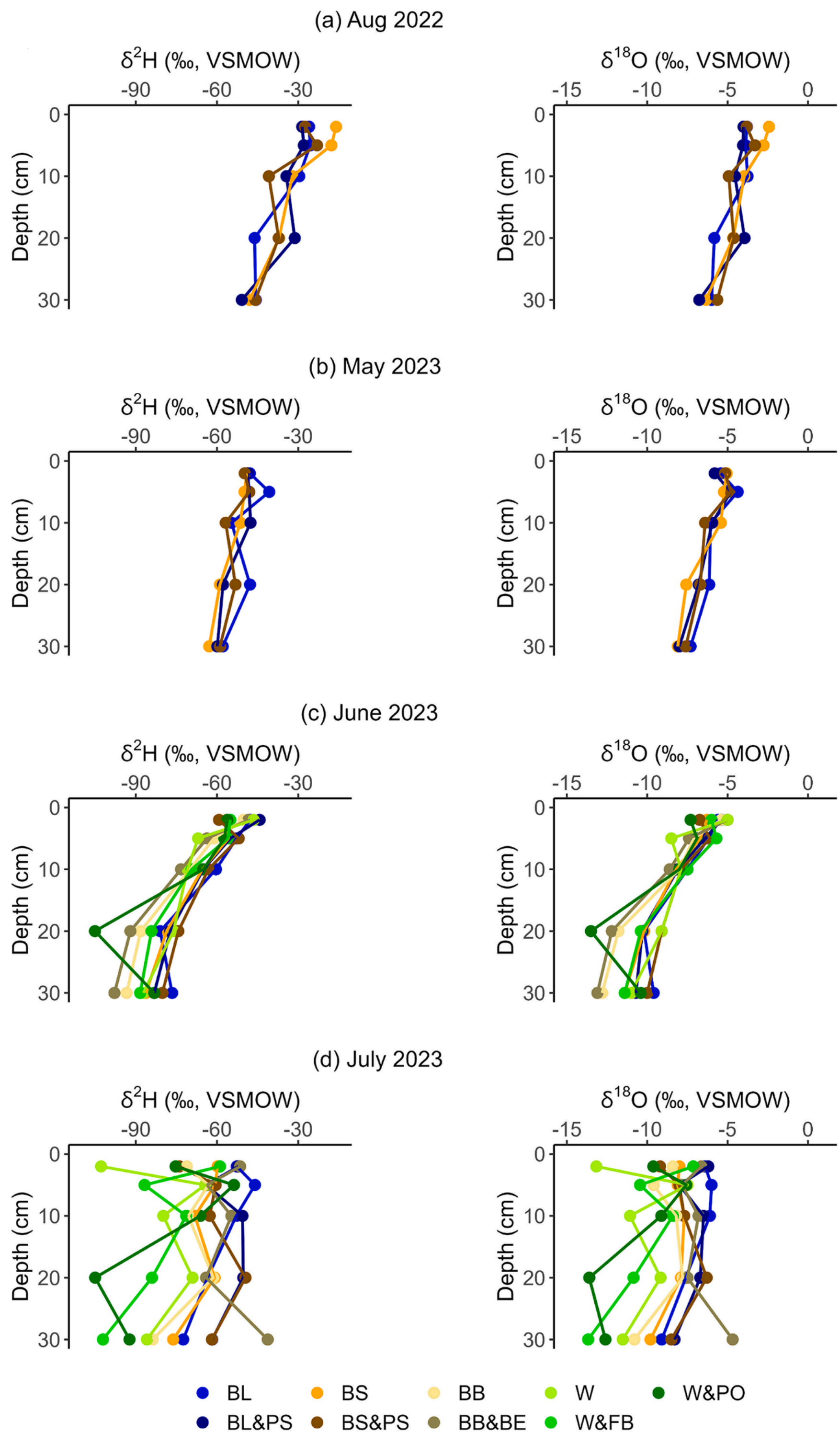

Fig. 5. Isotope composition of soil profile (0 – 30 cm) per cropping system for each sampling occasion. *BL* = Barley (Laureate) monoculture; *BL&PS* = Barley (Laureate) co-cropped with pea; *BS* = Barley (KWS Sassy) monoculture; *BS&PS* = Barley (KWS Sassy) co-cropping with pea; *BB* = Barley (Bere) monoculture; *BB&BE* = Barley (Bere) co-cropped with bean; *W* = Wheat monoculture; *W&FB* = Wheat co-cropped with faba bean; *W&PO* = Wheat co-cropped with pea.

during drought. This pattern has also been found in grassland species (*Centaurea jacea* L., *Phleum pratense, Lolium multiflorum, Poa pratensis, Taraxacum officinale, Trifolium repens, Rumex obtusifolius*) (Deseano Diaz et al., 2023; Prechsl et al., 2015; Wu et al., 2016). This behaviour could be attributed to the development of more fine roots of monoculture plant species in the shallow depths as an adaptation measure to drought (Deseano Diaz et al., 2023; Prechsl et al., 2015), which could have been the case of monoculture cereals in this study; though, root distributions and root densities were not measured.

4.2. *Effects of co-cropping on water uptake patterns*

In this study, barley and wheat in co-cropping generally responded to hydro-climatological conditions with a gradual proportional increase in

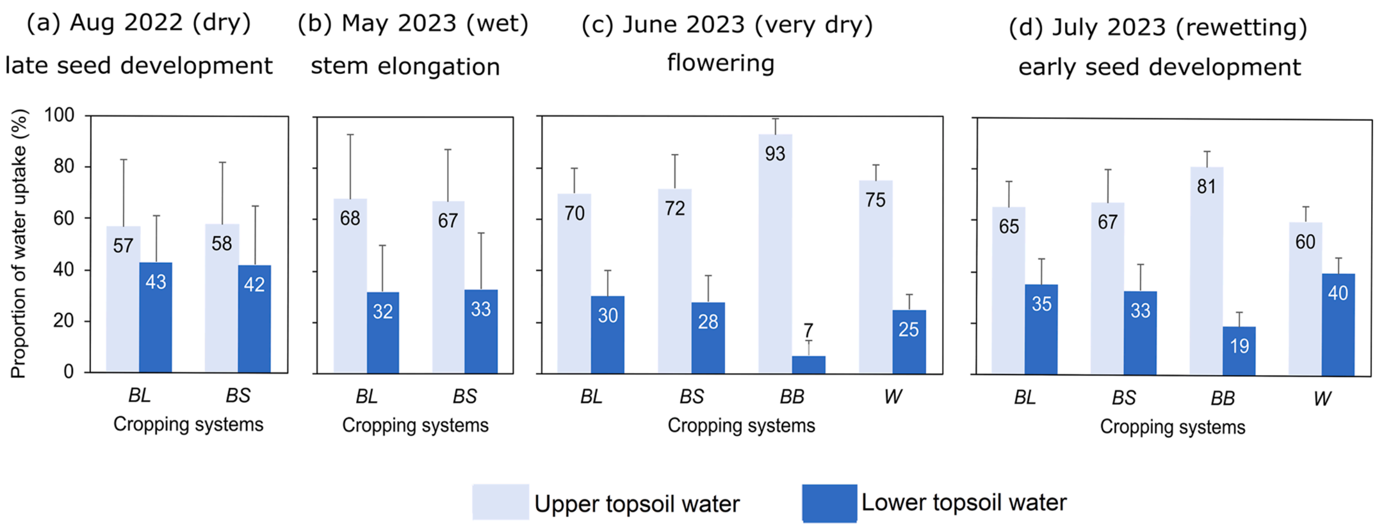

Fig. 6. Proportional contributions of soil water sources to plant water uptake for monocultures during all sampling occasions showing corresponding environmental condition and growth stages. *BL* = Barley (Laureate) monoculture; *BS* = Barley (KWS Sassy) monoculture; *BB* = Barley (Bere) monoculture; *W* = Wheat monoculture. Error bars represent 1 standard deviation of uncertainty.

lower topsoil water uptake, similar to findings in many agroecosystems and agroforestry in arid and tropical regions (Chen et al., 2018; Muñoz-Villers et al., 2020; Stomph et al., 2020; Yin et al., 2020; Zhang et al., 2022). However, previous studies on water uptake in temperate co-cropping systems and biodiverse grasslands showed ambiguous responses to water-limited conditions. For example, barley co-cropped with pea acquired water from deeper sources during wet conditions but shifted to upper topsoil (0–20 cm) during drought (Sun et al., 2022). Furthermore, Schmutz and Schöb (2023) observed that the water uptake proportion of wheat in mixtures remained unchanged compared to when grown alone, while barley in mixtures shifted their water uptake to shallower sources. This corresponds to the findings of Sun et al. (2022) and our own results for wheat co-cropped with pea (*W&PO*). While comparable results for co-cropping in similar climatic conditions are not available, there are parallels to findings in grassland environments. For example, Bachmann et al. (2015) observed no differences in water partitioning between diverse grassland communities and non-diverse grassland communities. Furthermore, Guderle et al. (2018) found that in diverse grassland, plants responded to dry upper soil conditions by taking up water from wetter and deeper soil depths, whereas species-poor assemblages did not change their uptake patterns.

The ambiguity found in these studies could be due to contrasts in drought intensities and how different plant species respond to water stress. For instance, in this study, the decline in precipitation amounts during the dry (August) and very dry (June) conditions compared to the long-term were ~20 % and ~16 %, respectively which are far less than ~36 % and ~34 % reductions observed in Schmutz and Schöb (2023) and Sun et al. (2022), respectively, which were also coupled with higher temperatures. Also, as discussed above, the soils here were relatively wet throughout, suggesting that the drought was relatively moderate for the cereal species in co-cropping during this study.

The observed modification in water uptake of co-cropped cereals in this study during different environmental conditions could be attributed to root water uptake plasticity. Root water uptake plasticity is the ability of plants to adjust their water uptake strategies by responding to varying water availabilities conditions (Fromm, 2019; Kühnhammer et al., 2020). Thus, allowing cereal plants in co-cropping to extend water acquisition to deeper sources where water was available especially when the upper topsoil was water-stressed (Homulle et al., 2021; Pigliucci, 2001; Schmutz and Schöb, 2023). This suggests that the legumes in this study might have responded to the moderate water stress, since legumes are found to be less drought resistant than cereals (Daryanto et al., 2017), and indirectly influenced the water uptake strategies of their cereal neighbours (Sun et al., 2022).

It was observed that the same wheat cultivar (WPB Escape) relied only on upper topsoil water when co-cropped with peas but moved to deeper layers when co-cropped with faba bean. This difference could be due to variations in neighbour-induced root behaviours of the two neighbouring legumes (Homulle et al., 2021; Zhang et al., 2020). This may suggest that water stress affected the faba beans and peas differently, resulting in a differential effect on the water uptake strategies of wheat. Further work is needed to reveal whether wheat co-cropped with pea could also exhibit root water uptake plasticity under more extreme dry conditions than observed in this study. Thus, raising further questions on the effect of prolonged, extreme and/or recurring drought on water dynamics of co-existing plant species in temperate climates.

Barley (KWS Sassy) co-cropped with pea showed most plasticity in terms of changing water uptake. This is consistent with previous findings that this cultivar is known to have root hairs and an extensive rooting structure that perform well during extreme weather conditions (Marin et al., 2021; Newton et al., 2020). This further indicates that the structure and plasticity of crop roots play crucial roles in complementarity of resource use and in designing efficient co-cropping systems (Stomph et al., 2020).

Overall, the findings of this study supported the hypothesis as expected that there are niche differences between water uptake of cereals in mono- and co-cropping but that these differences are less when compared to non-temperate climates. Although this study was based on a plot-scale experiment, the significant differences that were detected could nevertheless translate to substantial effects when scaled to field, farm, or national levels.

4.3. Limitations and opportunities for future research

This study provided new insights into the proportional water uptake of cereals in monocultures and co-cropping systems. However, it did not consider total water fluxes, which could have provided more insights into total water use and water use efficiency (WUE) of the co-cropping systems. In addition to changes in proportional water uptake from distinct sources, WUE in co-cropping has been shown to increase from 6 % to 45 %, depending on environmental conditions and management practice (Yin et al., 2020). Evidence from arid and semi-arid regions revealed that where crop combinations were designed based on the principle of resource complementarity traits, increased WUE occurred

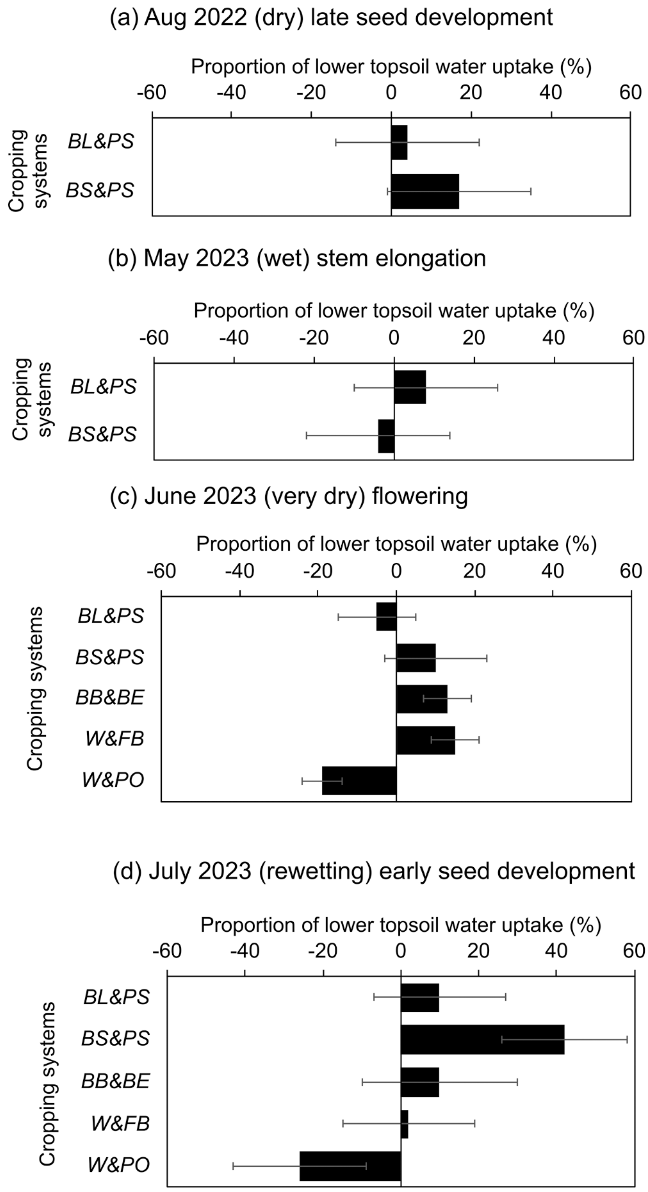

Fig. 7. Changes in the proportional contributions of lower topsoil water (5 – 30 cm) to plant water uptake in co-cropping systems compared with their respective monocultures during all sampling occasions showing corresponding environmental condition and growth stages. *BL&PS* = Barley (Laureate) co-cropped with pea; *BS&PS* = Barley (KWS Sassy) co-cropping with pea; *BB&BE* = Barley (Bere) co-cropped with bean; *W&FB* = Wheat co-cropped with faba bean; *W&PO* = Wheat co-cropped with pea. Error bars represent 1 standard deviation of uncertainty.

mainly via optimisation of the soil moisture use (Mao et al., 2012; Stomph et al., 2020). Future studies are therefore needed to evaluate the overall field performance and productivity of co-cropping in humid temperate environments to determine sustainable crop combinations.

It would also be interesting to explore facilitation effects and differences in plasticity of more plant species combinations, or cultivars with very different rooting traits. How these relate to other belowground processes, such as nutrient (nitrogen) and carbon dynamics at the field scale and interlink with water uptake in co-cropping would help to better understand the functioning of these systems under current and future climatic conditions. The use of modelling approaches to determine the crop (and cultivar) combinations that might be best in future temperate climate conditions could hereby be explored and provide solutions to predictions of drought to be more frequent in these environments (IPCC, 2023).

Finally, limitations to the water extraction method used need to be acknowledged. While the CVD extraction is the most used method to obtain soil and vegetation water for stable isotope analyses, there are several limitations associated with this technique, as summarised in a recent review by Ceperley et al. (2024). To interpret the δ^2H and δ^{18}O data in this study, potential artefacts that could be associated with the CVD extraction (Barbeta et al., 2020; Orlowski et al., 2018; Zuecco et al., 2022) were carefully considered. This included checking for spectral interferences and organic contamination after isotopic analyses of samples using a post-processing software (ChemCorrect™ by Picarro Inc.), and then checked for possible soil–xylem isotopic offsets prior to data interpretation. Although no plant or soil water samples were flagged for organic contamination, laser spectrometry as used in this study could still be susceptible to organic contamination, influence isotopic compositions and cause soil–xylem isotopic offsets (Ceperley et al., 2024; Millar et al., 2018). To validate the assumptions in MixSIAR and ensure the reliability of results, plant xylem data were ensured to be well within the soil water polygon, and significantly distinct end-members were used in the modelling.

4.4. *Broader implications*

This study revealed that water in the upper topsoil (upper 5 cm) could be much more critical to crop productivity in Scotland. This evidence-base is useful for farmers, land managers, water specialists and policy makers in Scotland for improving the efficiency of land and water management (Adams et al., 2022). Co-cropping cereals with legumes showed a modification of soil water uptake, hence presents a promising strategy for enhancing resilience and productivity with the potential to grow more food under increasingly frequent water limited conditions in Scotland (George et al., 2022). Hydro-climatological data have shown a trend towards lower soil moisture in early spring and longer recurring dry conditions in summer than previously observed. Co-cropping might therefore be beneficial for the distilling, food and feed industries which require stable and predictable yields, while also reducing the need for irrigation under extreme weather conditions (Allan et al., 2020; Gosling, 2014).

In the wider context, co-cropping combined with other Nature-based Solutions, such as reduced and no tillage, integrated cropping, cover crops and crop rotations, could promote enhanced nutrient use, reduced reliance on chemical inputs, climate change mitigation (Farooqi et al., 2020; George et al., 2022; Hawes et al., 2021), and support government net zero transition targets. It could also provide opportunities for diversifying crop production, optimizing land productivity, and improving biodiversity, thus offering a sustainable climate change adaptation practice in temperate agroecosystems (Brooker et al., 2023, 2021; Messean et al., 2021).

5. Conclusions

This research has provided new insights into cereal (barley and wheat) plant water uptake dynamics in humid temperate monoculture, and co-cropping systems. For the first time, data on soil and plant stable water isotopes have revealed that cereals in monocultures predominantly rely on upper topsoil water (<5 cm), regardless of cereal type growth stage and environmental conditions. Overall, when co-cropped, cereals exhibited root water uptake plasticity by altering their water uptake pattern via increased water acquisition from lower topsoil water (5 – 30 cm). This niche differentiation was found irrespective of the hydro-climatological conditions. These results suggest that co-cropping could potentially contribute to sustainable environmental management policies and climate change adaptation practices for agriculture in humid temperate regions through efficient water use.

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CRediT authorship contribution statement

Oludare S. Durodola: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Youri Rothfuss:** Writing – review & editing, Validation, Supervision, Resources, Methodology, Investigation. **Cathy Hawes:** Writing – review & editing, Supervision, Resources, Funding acquisition, Conceptualization. **Jo Smith:** Writing – review & editing, Supervision, Resources, Funding acquisition, Conceptualization. **Tracy Valentine:** Writing – review & editing, Resources, Funding acquisition, Conceptualization. **Josie Geris:** Writing – review & editing, Validation, Supervision, Resources, Methodology, Investigation, Funding acquisition, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2024.109439.

Data Availability

Data are publicly available to download from Durodola et al. (2024) available at doi:10.5281/zenodo.14529606.

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