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Drought Stress

# In-Field Evaluation of *Triticum spelta* and *Triticum aestivum* Performance Under Contrasting Irrigation Regimes and Farming Systems: Impact on Yield, Grain Quality and Soil Microbiota

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## ABSTRACT

Drought is a major abiotic stress affecting crop yields worldwide. Similarly, organic practices have been reported to enhance soil health and microbial diversity, influencing crop growth and yield. Given its drought tolerance, spelt (*Triticum spelta*) has been proposed as a resilient alternative to wheat (*Triticum aestivum*). Nevertheless, its agronomic and microbial responses under water-limited conditions within different farming systems remain poorly understood. This study compares wheat and spelt under irrigated and rainfed environments using conventional and organic farming practices in the field. Spelt showed greater resilience to water-limited conditions, maintaining yield, grain weight, and exhibiting higher antioxidant capacity under rainfed. Wheat yields dropped by 17% under rainfed but still remained 229% higher than spelt. Under organic farming, yields were 57%–85% and 77%–85% lower in spelt and wheat, linked to lower nitrogen availability. This provoked higher grain *C/N* ratios, indicating lower nutritional quality. Analysing belowground microbial ecosystem, farming practice was the primary factor explaining the dissimilarity of microbial community composition, with the irrigation regime playing a secondary role. Concretely, organic practices promoted the enrichment of soil bacterial microorganisms involved in nitrogen cycling and organic matter degradation, including members of Nitrosococcaceae SZB85, Thermomicrobiaceae, and *Actinomycetospora*; however, this was not enough to increase nitrogen availability and promote plant yield. On the other hand, under rainfed, specifically in conventional soils, the potentially pathogenic species *Ustilago maydis* increased, while both wheat and spelt simultaneously recruited beneficial species for plant development, *Chrysosporium pseudomerdarium*. Similarly, in organic soils experiencing water-limited conditions, an increase in beneficial microorganisms like *Paraphoma radicina* and *Rhizopus arrhizus* was also observed. Our findings highlighted the potential of spelt as a drought-tolerant alternative in water-limited regions while also revealing the limitations of organic farming practices for yield.

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**Key Points**

- Spelt maintains yield under rainfed environments compared to wheat, suggesting higher tolerance to water-limited conditions.
- Organic farming reduces yields by 57%–85% in wheat and spelt.
- Farming practice shapes microbial structure: enriching nitrogen- and organic matter-cycling bacteria in organic soils.
- Water limitation disrupts soil fungi by promoting pathogens, but simultaneously both crops recruit beneficial microbes.
- Despite spelt's resilience to water limitation, it had 220% lower yields than wheat.

## 1 | Introduction

Atmospheric $CO_2$ levels have been rising exponentially over recent decades and are projected to continue increasing by the end of the century (The Core Writing Team IPCC 2021). The increase in environmental $CO_2$ is expected to contribute to the expansion of arid regions worldwide, exacerbating the frequency and intensity of drought episodes (The Core Writing Team IPCC 2021). This is particularly concerning, given that drought is among the most severe abiotic stresses affecting conventional and staple crops such as wheat (*Triticum aestivum*). As a matter of fact, drought has been reported to significantly impair their growth and development at all stages (Gray and Brady 2016). Drought promotes stomatal closure and transpiration decrease in order to avoid water loss (Farooq et al. 2009). However, stomatal closure limits $CO_2$ uptake, impairs photosynthetic processes and promotes the overproduction of reactive oxygen species (ROS) when maintained for prolonged periods (Ahmad et al. 2018; Martínez-Goñi et al. 2024). To mitigate damage, plants accumulate compounds with antioxidant capacity, which are related to the nutritional quality of grains (Ragaee et al. 2006). Nevertheless, these mechanisms are not always sufficient, and long-term drought can lead to permanent damages in the photosynthetic apparatus, inhibition of photochemical reactions, vegetative growth, and ultimately cause yield losses of up to 76% (Gray and Brady 2016; Li et al. 2021). Given the intensification of drought events due to climate change and the global reliance upon conventional wheat (The Core Writing Team IPCC 2021; FAOSTAT 2025), finding alternative crops with enhanced resilience to water-limited conditions is essential for ensuring future food supply.

Alternative crops can be defined as crops that are not widely used on a global scale and/or crops that are primarily grown in specific regions but are less prevalent in global agriculture (Rodríguez et al. 2020; Martínez-Goñi et al. 2024). Spelt (*Triticum spelta*), an ancestral relative of wheat, has recently gained interest because of its high nutritional value and rich genetic diversity (Alvarez 2021). However, little is known about how spelt reacts to water limiting conditions, as the limited research conducted so far has produced contradictory results. In fact, some studies on several spelt varieties have shown spelt exhibits good resilience to water scarcity compared to wheat (Radzikowska et al. 2022; Kosakivska et al. 2023). Among the spelt varieties, Franckenkorn outstanded as a drought-tolerant variety, with little or no variation in its photosynthetic processes, as well as a greater accumulation of antioxidant molecules. In contrast, other research using Franckenkorn found extreme damages in its photosynthetic machinery when exposed to mild drought stress (Martínez-Goñi et al. 2023). These discrepancies may be due to the fact that these experiments were conducted in (semi)controlled environments, where variations in experimental conditions could have influenced the results (Lovell et al. 2016; Sales et al. 2022). Therefore, conducting field trials is crucial to better understand the tolerance of spelt to rainfed environments, particularly that of Franckenkorn variety, in comparison to wheat.

Together with drought episodes, another critical factor to consider when addressing the reduction in crop productivity is the employed agricultural production method. Currently, the majority of crops are grown using conventional farming practices, which rely heavily on the use of synthetic nitrogen- and phosphorus-based inorganic fertilisers to enhance yield. However, the excessive use of these fertilisers has been associated with the contamination and degradation of freshwater reserves and rivers, as documented in various regions globally (Datta et al. 1997; Qadri and Faiq 2020), as well as contributing to soil erosion (Pimentel et al. 1995). Similarly, conventional agriculture commonly employs pesticides to control pests, diseases, and weeds. A major drawback of these agrochemicals is their broad-spectrum and non-specific nature, which may result in harm to non-target organisms (Panico et al. 2022). In fact, the use of non-specific fungicides and bactericides not only targets pathogenic microorganisms but also disrupts the broader soil microbiota, including beneficial microorganisms (Hartmann et al. 2015). As a result, alternative farming practices, such as organic farming, have gained significant attention in recent decades (Smith et al. 2019; Zarraonaindia et al. 2020; Ghiglieno et al. 2023). Organic farming, defined by the absence of synthetic fertilisers and pesticides, usually leads to lower production in the short term, but it fosters a more resilient ecosystem and has long-term ecological benefits. In particular, among other benefits, it holds significant potential to improve soil health by enhancing the microbial diversity and richness (Smith et al. 2019), even though organic farming typically results in yields that are approximately 20% lower compared to conventional farming (de la Cruz et al. 2023).

In fact, soil microorganisms play a critical role in enhancing plant resilience to drought stress, making them vital for sustainable agriculture in water-limited environments. Beneficial microorganisms can improve drought tolerance by enhancing root architecture, facilitating water and nutrient uptake, modulating root exudation, maintaining soil structure and increasing soil water retention (Gu et al. 2024). Additionally, microbial communities can promote the accumulation of antioxidant compounds that protect plants from oxidative stress during water deficit (Kang et al. 2022). These interactions are particularly beneficial in organic farming systems, where the microbial diversity is often higher compared to conventional farming practices, leading to improved soil health and plant stress resilience (Lori et al. 2017). Understanding and harnessing the potential of soil-borne microorganisms could therefore provide key insights into

enhancing drought tolerance in crops like spelt, offering a more sustainable approach to crop production in a changing climate.

In summary, the intensification of drought events, the need for sustainable farming practices, and the potential of soil microbial communities to enhance drought resilience underscore the importance of exploring alternative crops like spelt. Therefore, this research aims to compare the tolerance to water-limited conditions of spelt and wheat in the field, examining their physiological responses, antioxidant capacity, and soil microbiota across two water regimes (irrigated and rainfed) and two agronomic systems (conventional and organic). We hypothesise that (1) the spelt variety Franckenkorn will produce lower yields than wheat due to its limited breeding for yield improvement. However, (2) spelt will demonstrate greater resilience to water-limited conditions compared to wheat by enhancing its antioxidant capacity. (3) Organic farming practices will increase soil microbial diversity relative to conventional farming, providing protection to water-limited conditions for both wheat and spelt, but despite these benefits, (4) yields under organic farming practices will be lower than those achieved under conventional farming.

## 2 | Materials and Methods

### 2.1 | Plant Material and Growth Conditions

Seeds of *Triticum aestivum* var. Florence Aurora (wheat) and *Triticum spelta* var. Franckenkorn (spelt) were sown at the experimental fields of NEIKER – Basque Institute for Agricultural Research and Development (Basque Country, Spain) in Arkaute (Basque Country, Spain). The conventional farming plot (C) was located at coordinates 42°51′02.4″ N 2°37′15.5″ W, while the organic farming plot (O) was situated at coordinates 42°50′59.9″ N 2°37′07.0″ W. The organic farming plot began its transition from conventional to organic farming in 2017 and was certified as organic in 2020 under European Union standards for organic soils (European Union 2018). This 3-year conversion period allowed for the complete leaching of any residual conventional agrochemicals, including fertilisers and pesticides. Throughout this time, all management practices adhered to organic standards, ensuring the development of soil characteristics specific to organic systems. By the time we conducted the experiment, the organic farming plot had been fully organic for 2 years. Sowing for both crops took place on February 10, 2022, and harvest occurred on August 18, 2022, marking 189 days after sowing (DAS). Environmental data for Table 1 were obtained from the website of the Basque Meteorological Agency and its weather station in Arkaute, Spain (EUSKALMET 2025). Average growth temperature, relative humidity and rain during the whole growth cycle were 14.27°C, 75% and 229.90 mm, respectively. Compared to the years between 2020 to 2024, 2022 was a drier and warmer year with 0.68°C higher temperature and 56 mm less precipitation (Table 1). Detailed daily averages for air temperature, relative humidity and total precipitation are provided in the (Table S1). Crop phenology was determined using the Zadoks scale (*Z*) (Zadoks et al. 1974), with specific growth stages for wheat and spelt provided in Table 2.

For each species and farming practice, each plot was divided into four subplots of 12 $m^2$, which were treated as independent

**TABLE 1** | Air temperature (*T*), relative humidity (*H*) and precipitation (Rain) per month in the region where wheat and spelt were grown for the years 2020–2024. For temperature and relative humidity, the row labelled "Avg" shows average values, while for precipitation it shows the total precipitation values over the months. The values for the year in which sampling occurred are highlighted in bold.

| Year- | 2020 | | | 2021 | | | 2022 | | | 2023 | | | 2024 | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Month** | ***T*** **(°C)** | ***H*** **(%)** | **Rain (mm)** | ***T*** **(°C)** | ***H*** **(%)** | **Rain (mm)** | ***T*** **(°C)** | ***H*** **(%)** | **Rain (mm)** | ***T*** **(°C)** | ***H*** **(%)** | **Rain (mm)** | ***T*** **(°C)** | ***H*** **(%)** | **Rain (mm)** |
| 10-Feb | 8.47 | 78.17 | 3.00 | 9.25 | 75.86 | 36.40 | **6.94** | **79.22** | **16.80** | 4.89 | 73.92 | 31.20 | 7.69 | 81.78 | 122.70 |
| Mar | 7.96 | 79.28 | 74.80 | 8.12 | 74.88 | 26.50 | **8.48** | **77.58** | **60.30** | 10.37 | 68.82 | 14.50 | 9.24 | 76.50 | 73.40 |
| Apr | 12.12 | 78.75 | 50.90 | 9.24 | 73.07 | 49.60 | **9.08** | **80.56** | **70.70** | 11.25 | 74.79 | 32.20 | 10.51 | 71.47 | 18.90 |
| May | 15.18 | 75.07 | 77.30 | 12.40 | 76.21 | 42.70 | **15.39** | **75.01** | **10.20** | 13.05 | 76.88 | 35.70 | 12.18 | 79.49 | 101.20 |
| Jun | 15.98 | 77.28 | 45.80 | 16.23 | 79.85 | 70.50 | **18.34** | **74.03** | **13.80** | 18.14 | 78.75 | 54.50 | 15.77 | 82.23 | 51.30 |
| Jul | 18.80 | 73.26 | 8.80 | 17.89 | 75.07 | 2.50 | **20.42** | **68.21** | **23.40** | 18.70 | 75.68 | 71.50 | 18.43 | 77.21 | 17.90 |
| 18-Aug | 19.94 | 73.85 | 21.40 | 19.50 | 71.24 | 0.60 | **21.30** | **70.10** | **34.70** | 19.50 | 71.24 | 0.60 | 20.13 | 75.57 | 5.80 |
| Avg | 14.06 | 76.52 | 282.00 | 13.23 | 75.17 | 228.80 | **14.27** | **75.00** | **229.90** | 13.70 | 74.30 | 240.20 | 13.42 | 77.75 | 391.20 |

**TABLE 2** | Phenological growth stages of wheat and spelt under conventional (C) and organic (O) farming systems. Growth and phenological stages are indicated based on the Zadoks scale.

| | Wheat C | | Wheat O | | Spelt C | | Spelt O | |
|---|---|---|---|---|---|---|---|---|
| **Date** | **Zadoks** | **Phenology** | **Zadoks** | **Phenology** | **Zadoks** | **Phenology** | **Zadoks** | **Phenology** |
| 10/02/2022 | 00 | Dry seed | 00 | Dry seed | 00 | Dry seed | 00 | Dry seed |
| 20/03/2022 | 20–25 | Tillering | 20–25 | Tillering | 20–25 | Tillering | 20–25 | Tillering |
| 10/04/2022 | 31 | First node | 29–31 | Tillering complete/First node | 29–31 | Tillering complete/ First node | 29–31 | Tillering complete/First node |
| 17/05/2022 | 55–59 | Ear half/fully emerged | 55 | Ear half emerged | 45 | Boot swollen | 41 | Flag leaf sheath extending |
| 02/06/2022 | 65 | Anthesis half-way | 59 | Ear fully emerged | 59 | Ear fully emerged | 55–59 | Ear half/fully emerged |
| 09/06/2022 | 71 | Watery ripe | 65 | Anthesis half-way | 65 | Anthesis half-way | 59–65 | Ear fully emerged/ Anthesis half-way |
| 15/06/2022 | 75–83 | Medium milk/ Early dough | 71–75 | Watery ripe/Medium milk | 71 | Watery ripe | 65–71 | Anthesis half-way/ Watery ripe |
| 07/07/2022 | 87 | Hard dough | 83–85 | Early/Soft dough | 75–83 | Medium milk/Early dough | 75 | Medium milk |
| 14/07/2022 | 91 | Grain hard | 85–87 | Soft/Hard dough | 85–87 | Soft/Hard dough | 85–87 | Soft/Hard dough |
| 28/07/2022 | 92 | Harvest ripe | 92 | Harvest ripe | 92 | Harvest ripe | 92 | Harvest ripe |
| 18/08/2022 | 99 | Harvested product | 99 | Harvested product | 99 | Harvested product | 99 | Harvested product |

biological replicates. Similarly, half of the plots for each species and treatment were designated as irrigated (I), receiving consistent irrigation, while the remaining plots relied solely on natural precipitation (rainfed, R). Overall, the irrigated plots received 2166.03 $m^3$/ha of irrigation water in addition to 2299.00 $m^3$/ha from precipitation, while the rainfed plots relied solely on the 2299.00 $m^3$/ha provided by precipitation. During the experiment, the driest and hottest months coincided with the reproductive stage of wheat and spelt (Z55-92), a phase highly sensitive to water scarcity (Gray and Brady 2016).

Before sowing, conventional plots received an application of 176 mL/ha of TALLIT Super (IQV Mat Holding Group, Spain) and Biathlon 4D (BASF, Germany) herbicides for weed control. In organic plots, weed control was carried out with a flexible tine harrow. At 19 DAS, approximately coinciding with the first leaf stage (Z10), conventional plots received an initial fertilisation of 400 kg/ha of 8-15-15 NPK. This was followed by a supplementary application of 400 kg/ha of NAC27 at 69 DAS, when plants were in the late tillering to early stem elongation phase (Z29-31), to ensure adequate nutrient availability. In contrast, organic plots were neither fertilised nor supplemented, as they were nutrient-rich due to a prior cover cultivation of crotalaria. Detailed soil nutrient status prior to fertilisation is provided in Table 3.

In total, the experiment consisted of 32 subplots, with four replicates for each combination of farming practice, irrigation system and crop species. Farming practices and irrigation systems were named as follows: conventional irrigated, CI; conventional rainfed, CR; organic irrigated, OI; organic rainfed, OR.

**TABLE 3** | Characteristics of the soil for the plots under conventional and organic farming practices.

| Data | Conventional | Organic |
|---|---|---|
| pH | 8.4 | 8.6 |
| Texture | Clay loam | Clay loam |
| Effective Cation Exchange Capacity (meq 100 $mL^{-1}$) | 36.4 | 52.7 |
| Electrical conductivity in calcium sulphate ($\mu S\ cm^{-1}$) | 1960 | 1960 |
| Carbonates (% $CaCO_3$) | 34% | 10.90% |
| C/N ratio | 10 | 9.5 |
| Oxidisable organic matter | 2.93% | 3.10% |
| Kjeldahl nitrogen | 0.17% | 0.19% |
| Extractable phosphorus in bicarbonate (mg P $L^{-1}$) | 31 | 37 |
| Extractable potassium in ammonium nitrate (mg K $L^{-1}$) | 267 | 359 |
| Extractable magnesium in ammonium nitrate (mg Mg $L^{-1}$) | 98 | 210 |
| Extractable sodium in ammonium nitrate (mg Na $L^{-1}$) | < 20 | 23 |
| Nitrate nitrogen (mg N-$NO_3$ $L^{-1}$) | 47 | 29 |
| Extractable calcium in ammonium nitrate (mg Ca $L^{-1}$) | 6960 | > 10,000 |
| Cadmium (mg Cd $kg^{-1}$ DW) | < 0.7 | 0.96 |
| Chromium (mg Cr $kg^{-1}$ DW) | 39.5 | 71.6 |
| Copper (mg Cu $kg^{-1}$ DW) | 6.02 | 7.59 |
| Nickel (mg Ni $kg^{-1}$ DW) | 17.2 | 29.9 |
| Zinc (mg Zn $kg^{-1}$ DW) | 50.1 | 63 |

## 2.2 | Measurement of Agronomic Traits

Plant *Height* was measured at 159 DAS (Z75-92), approximately 1 month before harvest, when the plants had reached their maximum height. Harvesting took place at 189 DAS (Z99), and *Yield* was calculated by dividing the total grain production per subplot by the 12 $m^2$ area of that subplot. Additionally, the *100-grain weight* was determined by weighing 100 grains from each subplot.

## 2.3 | Measurement of C/N Ratio, Antioxidant Capacity and Phenols

The grains were ground as explained by (Pérez-López et al. 2015). Briefly, grains were ground to a fine powder using the automatic mill MM400 (Retsch, Germany). Subsequently, 0.002 g dry weight of grains were used to determine carbon (C) and nitrogen (N) content using an elemental analyser (FlashEA 1112; ThermoFinnigan, Germany). Samples were weighed in a tin capsule and introduced into a quartz reactor containing $WO_3$ and copper, which is heated to 1020°C. The combustion gas mixture is carried by a helium flow to a $WO_3$ layer to ensure complete quantitative oxidation, followed by a reduction step in a copper layer to convert nitrogen oxides and $SO_3$ to $N_2$ and $SO_2$. The resulting components ($N_2$, $CO_2$, $H_2O$ and $SO_2$) are separated in a chromatographic column and detected by a thermal conductivity detector.

For the extraction of antioxidants and phenols 0.170 ± 0.008 g of grain powder was weighed and placed into microtubes. Extraction was then performed by adding 600 µL of acetone (50%) to each microtube. The mixture was thoroughly homogenised using a vortex and the samples were then sonicated for 30 min using a SONOREX SUPER RK 156 (BANDELIN electronic GmbH & Co. KG, Germany). After sonication, the samples were centrifuged for 15 min at 4°C. The supernatant and pellet were separated, with the supernatant transferred to new microtubes.

To determine phenolic content, the Folin–Ciocalteu method was applied (Ainsworth and Gillespie 2007). Specifically, the initial extract was diluted four times by mixing 100 µL of the sample with 400 µL of acetone. For this measurement, a calibration

curve based on gallic acid in acetone was used. Fifty microliters (50 μL) of the diluted sample and the calibration standards were pipetted into a microplate. Next, 100 μL of diluted Folin reagent was added, and the mixture was incubated for 5 min. The Folin reagent was prepared in advance by diluting 1.2 mL of the concentrated Folin reagent with 10.8 mL of water. After the 5-min incubation, 400 μL of 700 mM sodium carbonate was added, and the mixture was incubated for 1 h in the dark. After 1 h, the microplate was centrifuged for 5 min, and 200 μL of the resulting supernatant was pipetted into the plate wells. The absorbance of the plate was measured at 765 nm using a spectrophotometer.

Antioxidant capacity was measured using the ferric ion reducing antioxidant power (FRAP) method (Benzie and Strain 1996). Briefly explained, the FRAP reagent was prepared by dissolving 2,4,6-tris(2-pyridyl)-s-triazine (TPTZ) in 40 mM HCl, followed by addition of 20 mM $FeCl_3$ and acetate buffer (pH 3.6) in a 1:1:10 ratio. Samples were mixed with FRAP reagent (1:1:25 ratio of extract:PBS:FRAP), incubated (6 min, dark) and centrifuged (5 min, 15,000×*g*, 4°C) to clarify turbidity. Absorbance was measured at 593 nm using a spectrophotometer against a Trolox (1 mM) calibration curve. Antioxidant capacity was expressed as μmol FRAP $g^{-1}$ DW.

## 2.4 | Statistical Analysis

SPSS software version 28.0.1.1 for Windows (IBM Corp, Armonk, NY USA) was used to conduct statistical analysis. The influence of species (wheat and spelt), irrigation system (irrigated and rainfed), farming practice (conventional and organic) and their interaction upon agronomic traits and grain *C/N*, antioxidant capacity and phenol values were analysed by three-way ANOVA. Means were compared using Duncan's multiple range test, and values $p < 0.05$ were considered to be statistically significant. The studied agronomic measurements were visualised using GraphPad Prism software version 8.2.1 (GraphPad Software, San Diego, CA USA, www.graphpad.com).

## 2.5 | Characterisation of Soil Microbial Communities

### 2.5.1 | Sampling

Three soil samples were collected from each subplot using a soil corer, collecting the first 0–15 cm soil layer close to the roots. The soil from each subplot was pooled, homogenised, and stored at 4°C until the completion of the sampling process. Subsequently, the samples were preserved at −20°C until further analyses.

### 2.5.2 | DNA Extraction and Amplicon Sequencing

DNA was extracted with the DNeasy PowerLyzer PowerSoil Kit (QIAGEN). The internal transcribed spacer 2 region (ITS2) was amplified with fITS7/ITS4 primers (GTGARTCATCGAATCTTTG/TCCTCCGCTTATTGATATGC) (Ihrmark et al. 2012), and the V3-V4 hypervariable region of the gene 16S rRNA was amplified with primers 341F/805R (CCTACGGGNGGCWGCAG/GACTACHVGGGTATCTAATCC) (Klindworth et al. 2013). Dual indexing of amplicons was performed using Nextera XT index kit v2; libraries were purified using the CleanNGS kit (CleanNA, Waddinxveen, Netherlands), and sequencing was conducted independently in a MiSeq Illumina sequencer at the Genotyping Service of the University of the Basque Country (SGIKER) using the MiSeq Reagent Kit v2. Paired-end sequencing (PE) was performed with a 2×300 bp read length configuration, corresponding to 600 sequencing cycles (PE 2×300 bp, 600 cycles).

### 2.5.3 | Raw Data Processing and Statistical Analysis

Raw sequences were quality trimmed and demultiplexed in QIIME 2 (Bolyen et al. 2019). Only forward reads were retained for downstream analyses, as quality filtering of reverse reads resulted in a high loss of data and poor merging efficiency. DADA2 was used for denoising, chimera removal and amplicon sequence variant (ASV) determination. The sequence variants were assigned to species by performing taxonomic classification against the Silva 132 database (prefiltered for the 16S rRNA V3-V4 region) for bacteria, while the UNITE v8_04.02.2020 was used for the fungal fraction. Visual and statistical analysis of bacterial and fungal data was also conducted in QIIME 2. Diversity metrics, alpha and beta, were computed using the qiime diversity core-metrics-phylogenetic pipeline, with a sampling depth of 34,000 reads for ITS and 39,600 for 16S datasets. The alpha diversity of each sample was determined based on Observed Otus' (richness) and Shannon's (a combined measure of richness and evenness) indexes, and the non-parametric Kruskal-Wallis test was used to assess significant differences between the factors studied and the mentioned indexes. Community composition was assessed through Bray-Curtis (that accounts for species abundances) and Jaccard (that accounts for species presence/absence) indexes (Hao et al. 2019) and compositional differences between studied conditions were determined using the Pairwise Permanova test. Differentially abundant microbial taxa across treatments were identified using Linear Discriminant Analysis Effect Size (LEfSe) (Segata et al. 2011), which detects taxa that are both statistically significant and biologically relevant. Correlation analysis between plant parameters and microbial profiles was conducted in R with the ggcorrplot package using Pearson's statistic. In addition, microbiota and crop performance parameters relationship was studied through a Non-metric Multidimensional Scaling (NMDS) analysis. A Hellinger transformation was applied to the abundance matrix of 16S rRNA data before computing the ordination. Crop performance parameters were incorporated into the NMDS by fitting them as vectors using function envfit (Lozupone and Knight 2005).

# 3 | Results

## 3.1 | Comparative Analysis of Wheat and Spelt Performance Across Irrigation System Within Conventional Farming Practices

*Height* and *Yield* exhibited contrasting trends under conventional irrigated (CI) conditions, with spelt showing significantly greater *Height* but lower *Yield* compared to wheat (Table 3 and Figure 1A,B). Specifically, while spelt exhibited

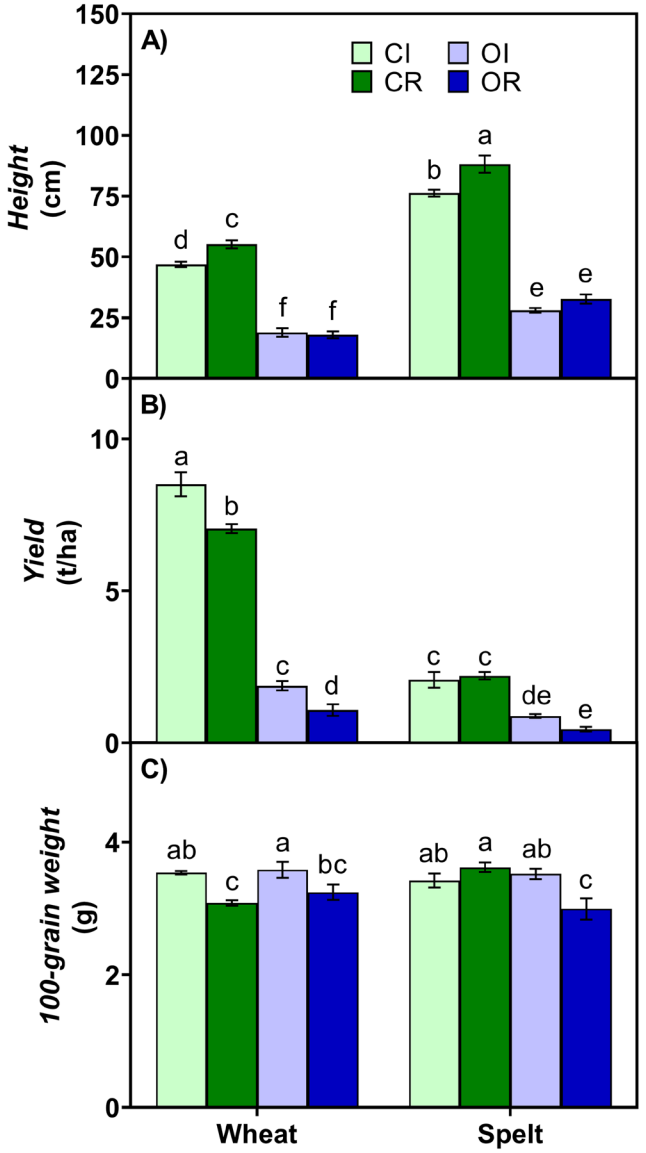



**FIGURE 1** | Effect of species, irrigation system and farming practices in (A) *Height*, (B) *Yield* and (C) *100 seed weight*. Conventional irrigated (CI), conventional rainfed (CR), organic irrigated (OI) and organic rainfed (OR) are indicated as light green bars, dark green bars, light blue bars and dark blue bars, respectively. Each bar represents mean ± standard error (S.E.) of four replicates. Different letters are used to represent values significantly different between treatments and species ($p < 0.05$).

average values of *Height* and *Yield* of 77 cm and 2.08 t/ha, respectively, wheat displayed average values of 47 cm in *Height* and 8.51 t/ha in *Yield*. Interestingly, under conventional rainfed (CR) conditions, wheat and spelt increased *Height* by 17.55% and 15.62%, respectively, compared to CI (Figure 1A). On the contrary, trends for yield differed between species, with values in spelt remaining unchanged, while in wheat, yield decreased from 8.51 to 7.06 t/ha (Figure 1B). Despite water-limited conditions not affecting *Yield* of spelt, it is important to note that the average *Yield* values in spelt were 2.15 t/ha, 70%–75% lower than in wheat regardless of CI or CR (Figure 1B). Lastly, we found that *100-grain weight* was statistically similar between both species under CI, with average values of 3.48 g (Table 3 and Figure 1C). However, under CR conditions, wheat experienced a significant decrease of 12.87%, while spelt maintained statistically similar values (Figure 1C).

Regarding physiological and biochemical traits, we found species to have an influence on grain *Phenols*, *Antioxidant capacity* and *C/N*, but the irrigation system only affected *Phenols* (Table 4, Figure 2A,B and Figure 3). As a matter of fact, we found *Phenols* to be significantly higher in wheat with average values of 5.47 μmol galic acid $g^{-1}$ DW, although they were significantly decreased by 12.5% upon exposure to CR (Figure 2A). In contrast, *Phenols* values remained similar between CI and CR in spelt, with average values of 4.60 μmol galic acid $g^{-1}$ DW (Figure 2A). Similarly, *Antioxidant capacity* values were statistically similar between species under CI (Figure 2B). Nonetheless, under CR conditions, wheat exhibited a significant decrease of 12.93%, whereas spelt showed an increase of 10.30% (Figure 2B). Finally, the *C/N* ratio was significantly higher in wheat under CI conditions, with an average value of 22, compared to the significantly lower value of 16.5 observed in spelt, and values did not vary under CR (Figure 3).

### 3.2 | Comparative Analysis of Wheat and Spelt Performance Across Irrigation System Within Organic Farming Practices

The interaction among species, irrigation system and farming practice had an effect in *Yield* and *100-grain weight*, but not in *Height* (Table 4). As a matter of fact, *Height* was significantly

**TABLE 4** | Three-way ANOVA for crop species (Sp, wheat and spelt), irrigation system (*I*, irrigated and rainfed), farming practice (*F*, conventional and organic) and their interaction for agronomic traits and grain quality variables.

| | Species (Sp) | Irrigation system (*I*) | Farming practice (*F*) | Sp×*I* | Sp×*G* | *I*×*F* | *S*×*I*×*F* |
|---|---|---|---|---|---|---|---|
| Height | *** | *** | *** | ns | *** | ** | ns |
| Yield | *** | *** | *** | ** | *** | ns | * |
| 100-grain weight | ns | *** | ns | ns | * | * | ** |
| Phenols | ** | *** | *** | ns | ** | ns | ns |
| Antioxidant capacity | *** | ns | ns | *** | ns | ns | ns |
| C/N ratio | *** | ns | *** | ns | ns | ns | ** |

*Note:* Results are represented as ns (non-significant), * ($p < 0.05$), ** ($p < 0.01$), and *** ($p < 0.001$).

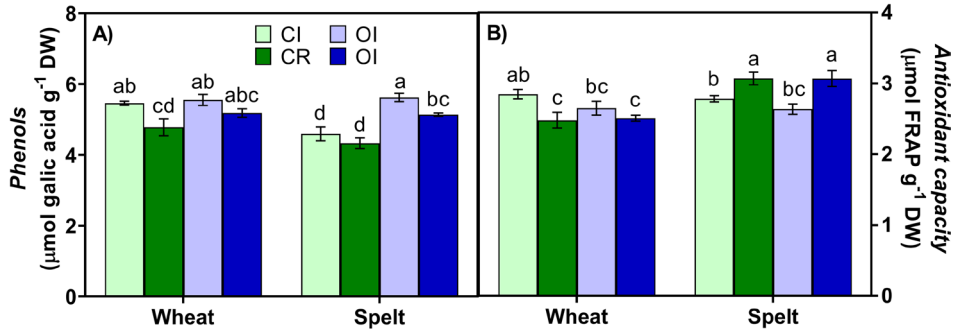



**FIGURE 2** | Effect of species, irrigation system and farming practices in (A) *Phenols* and (B) *Antioxidant capacity*. Each bar represents mean ± standard error (S.E.) of four replicates. Treatments and statistical analysis are explained in Figure 1. Different letters are used to represent values significantly different between treatments and species ($p < 0.05$).

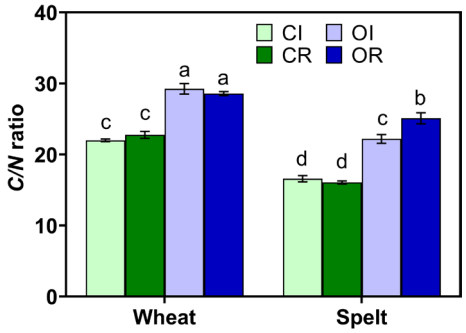



**FIGURE 3** | Effect of species, irrigation system and farming practices in *C/N* ratio. Each bar represents mean ± standard error (S.E.) of four replicates. Treatments and statistical analysis are explained in Figure 1. Different letters are used to represent values significantly different between treatments and species ($p < 0.05$).

decreased under organic practice by 63%–64%, irrespective of the species and irrigation system (Figure 1A). In the same manner, *Yield* was significantly decreased in both species upon exposure to OI and OR, even though the impact was greater in wheat than in spelt (Figure 1B). Specifically, *Yield* was decreased by 77.92% and 84.66% in wheat under OI and OR when compared to *Yield* values under CI and CR, respectively. On the contrary, in spelt the decrease was 57.37% and 79.49%, respectively.

Farming practice alone influenced *Phenols* and *C/N*, but not *Antioxidant capacity* (Table 4). Similarly, the interaction between species and practice only influenced *Phenols*, whereas the combined interaction of species, irrigation system and practice affected only the *C/N* ratio (Table 4). In fact, *C/N* ratio was significantly increased by 30.67% in wheat and 36.92% in spelt when exposed to OI (Figure 3). While the *C/N* ratio in wheat remained unchanged under OR, in spelt, it increased by 13.15% in comparison with OI. Likewise, *Phenols* in wheat had statistically similar values under OI and OR than those observed under CI and CR, respectively (Figure 2A). In contrast, spelt significantly increased the *Phenols* under both OI and OR, particularly under OI, where values reached 5.63 µmol gallic acid $g^{-1}$ DW. Despite this increase, the *Phenols* values of spelt under OI and OR conditions remained similar to those reported in wheat. The last quality trait, *Antioxidant capacity*, was reduced in wheat under OI conditions compared to CI, with values similar to those observed under CR and OR (Figure 2B). In spelt, however, *Antioxidant capacity* values under OI and OR followed a similar trend to those observed under CI and CR, respectively.

### 3.3 | Soil Microbiota Profile Analysis of Wheat and Spelt Across Irrigation System

The soil of both crops had similar fungal alpha diversity values in the irrigated condition, while slight significant differences on bacterial Shannon values were observed, the diversity being higher in spelt (10.25 vs. 9.66 in spelt and wheat respectively, $p = 0.043$). However, neither bacterial nor fungal community composition differed between the two plant species within CI condition (Pairwise Permanova $p > 0.05$), with both crops sharing the same 10 most abundant groups (fungi: Euromycetes, Glomeromycetes, Leotiomycetes, Agaricomycetes, Mortierellomycetes, Tremellomycetes, Dothideomycetes, Sordariomycetes; bacteria: Chloroflexi, Verrucomicrobiae, Phycisphaerae, Bacteroidia, Actinobacteria, Gammaproteobacteria, Thermoleophilia, Planctomycetacia, Alphaproteobacteria, Acidobacteria).

While species did not have a significant role on microbiota structure under irrigated conditions, significant differences in diversity and community composition between two water regimes were evident within each crop. In conventionally managed soils, irrigation regime had a stronger effect on spelt soils, with the bacterial diversity and fungal evenness being significantly higher under the irrigated condition (Figure 4A1,B2). Within organic soils, however, the opposite trend was observed, where overall irrigated soils had lower diversity than rainfed soils in both crops, although it was statistically significant only for the bacterial Shannon Index comparison of wheat (OI vs. OR $p < 0.05$, Figure 4A2).

In terms of community composition, both crops showed significant differences in their bacterial and fungal communities between irrigated and rainfed treatments within each farming practice. The dissimilarity analyses were based on the Bray-Curtis index, which incorporates the relative abundance of species and captures variations related to both species presence and their proportions within each community (thereby highlighting the influence of dominant species on overall structure), and the Jaccard index, which relies solely on presence/absence data, demonstrating that qualitative species diversity also contributes consistently to dissimilarity. The coincidence in the statistical significance of both indices (Table 5:

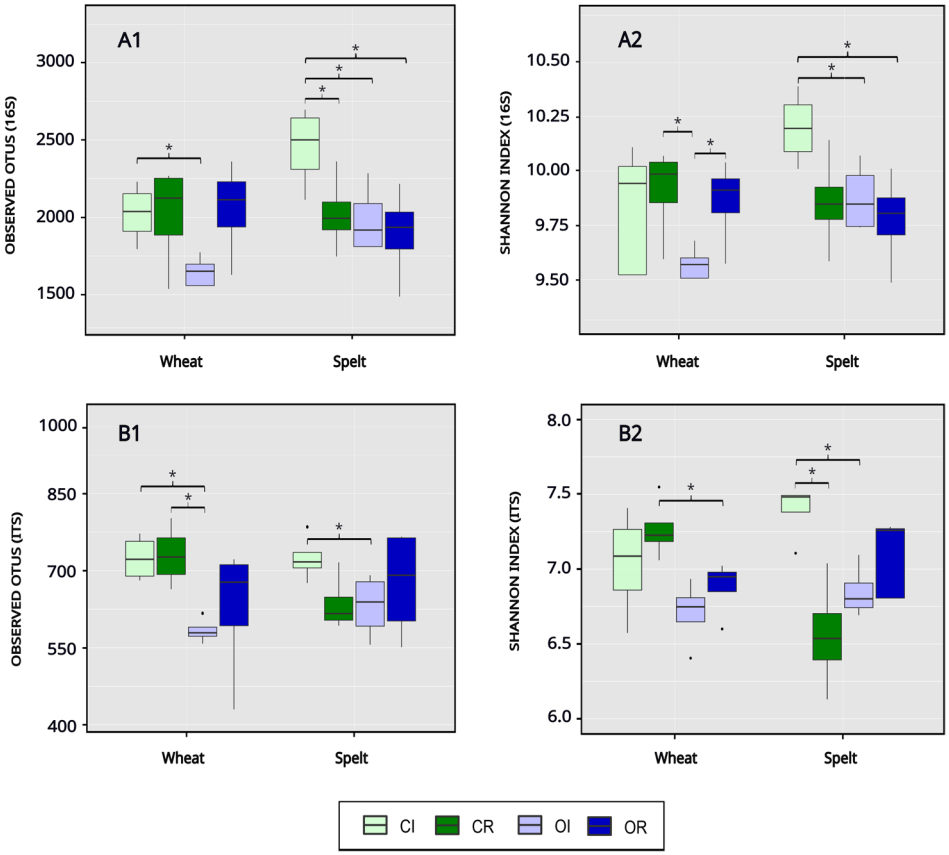



**FIGURE 4** | Effect of irrigation and farming practice in (A) bacterial (B) and fungal communities' alpha diversity. The metrics represented are the Observed Otus (A1, B1) and the Shannon index (A2, B2). The Pairwise Kruskal-Wallis test was used for statistical analysis and significant differences are represented as $*p < 0.05$. Conventional irrigated (CI), conventional rainfed (CR), organic irrigated (OI) and organic rainfed (OR) are indicated as light green bars, dark green bars, light blue bars and dark blue bars, respectively.

**TABLE 5** | Pairwise PERMANOVA results comparing bacterial and fungal communities across treatments in wheat and spelt. Pseudo-*F* values and corresponding *p* values are shown for Bray-Curtis and Jaccard dissimilarity indices.

| | | Bacterial community | | | | Fungal community | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | Bray-Curtis | | Jaccard | | Bray-Curtis | | Jaccard | |
| **Species** | **Treatment pairwise** | **Pseudo-*F*** | ***p*** | **Pseudo-*F*** | ***p*** | **Pseudo-F** | ***p*** | **Pseudo-*F*** | ***p*** |
| Wheat | CI vs. CR | 1.523 | 0.023 | 1.350 | 0.026 | 1.912 | 0.043 | 1.355 | 0.011 |
| | OI vs. OR | 1.667 | 0.019 | 1.399 | 0.025 | 2.033 | 0.026 | 1.306 | 0.029 |
| | CI vs. OI | 5988 | 0.023 | 3.385 | 0.023 | 6.28 | 0.031 | 3.108 | 0.030 |
| | CR vs. OR | 6.058 | 0.025 | 3.008 | 0.023 | 4.943 | 0.024 | 2.537 | 0.029 |
| Spelt | CI vs. CR | 1.778 | 0.036 | 1.505 | 0.030 | 2.345 | 0.035 | 1.330 | 0.026 |
| | OI vs. OR | 1.344 | 0.025 | 1.154 | 0.027 | 1.492 | 0.034 | 1.362 | 0.035 |
| | CI vs. OI | 5.803 | 0.029 | 3.264 | 0.026 | 5.478 | 0.031 | 2.628 | 0.030 |
| | CR vs. OR | 6.132 | 0.047 | 2.954 | 0.022 | 4.568 | 0.034 | 2.561 | 0.024 |

*Note:* Treatments: CI, conventional irrigated; CR, conventional rainfed; OI, organic irrigated; OR, organic rainfed.

$p < 0.05$ in Bray-Curtis and Jaccard, comparing CI vs. CR and OI vs. OR) suggests that the observed variation in community composition reflects changes in both species abundance and presence/absence. Therefore, the variation between treatments is consistent across different analytical approaches, providing a more complete description of community structure.

### 3.4 | Soil Microbiota Profile Analysis of Wheat and Spelt Across Farming System

Irrigated wheat and spelt soils showed significantly higher bacterial and fungal richness under conventional practice than in the organic one. In the case of bacteria, this comparison was

statistically significant in spelt species for both alpha diversity indexes (Figure 4A1,A2). However, in wheat, only the Observed Otus index comparison was found to be significant, with mean values of 1776 and 1355 in CI and OI, respectively. Similarly, in fungi, both alpha diversity indexes were highest in the CI condition compared to that in OI in spelt (Figure 4B1,B2), while in wheat, only the Observed Otus metrics showed such statistical significance (724 for CI and 583 for OI, respectively).

A different trend was observed when comparing farming practice within rainfed environments (CR vs. OR, $p > 0.05$), as no differences in alpha diversity were observed for any of the crops between conventional and organic practice, nor in bacteria nor in fungi, except for the comparison of the fungal Shannon index in wheat (Figure 4B2) where OR had less richness than CR.

However, regardless of the irrigation regime, community composition was significantly influenced by farming practices in both crops. As with the irrigation condition as a factor, both beta diversity indices were again statistically significant (Table 5: $p < 0.05$ in Bray-Curtis and Jaccard comparing CI vs. OI and CR vs. OR), confirming the robustness of the differences observed in the bacterial and fungal communities composition. Notably, the Pseudo-F values obtained from Pairwise Permanova analyses (Table 5) were significantly higher for the ¨farming¨ comparison (CI vs. OI and CR vs. OR) than for ¨irrigation¨ comparisons (CI vs. CR and OI vs. OR), indicating a stronger statistical effect for the former. In addition, the NMDS analysis (Figure 5) also showed that farming practice was the main driver explaining both bacterial and fungal community structure dissimilarities, being the irrigation system a secondary factor. According to the NMDS plot, *Phenols* and especially *C/N* ratio were more related to the organic treatment, while *Height* and *Yield* parameters were associated with conventionally grown soils, in both bacterial and fungal studies.

Due to these shifts in microbial community structure driven by farming practices and irrigation systems, a large number of differentially abundant taxa were identified in both crops (Figures S2, S3). Additionally, it is worth noting that within each combination of farming and irrigation conditions (CI, CR, OI, and OR), several significantly enriched groups were shared between the crops. For instance, among the bacterial taxa, spelt and wheat shared 38.2% of their enriched groups under the CI condition, compared to 16.5% in CR, 11.6% in OI, and 19.7% in OR. A similar trend was observed for the fungal biomarkers, with the CI condition showing the highest overlap between the crops (39%), while 16.8% of enriched taxa were common for CR, 31.6% for OI, and 28.2% for OR.

More specifically, Linear Discriminant Analysis Effect Size (LEfSe) identified the main bacterial and fungal taxa enriched in each treatment and shared by both crops, serving as biomarkers of each farming management and irrigation combination. In conventional soils (Table 6), the five bacterial taxa most strongly associated (highest LDA) with the irrigated condition (CI) belonged to *Pirellula*, Solirubrobacterales, Pedosphaeraceae, *Conexibacter*, and *Terrimicrobium*, while within the fungal community, members of *Claroideoglomus*, *Didymella*, and *Ramicandelaber*, as well as the species *Humicola fuscoatra* and *Funneliformis geosporum* were identified. On the contrary, conventional rainfed (CR) soils (Table 6) were significantly more abundant in members of Geminicococcaceae and Tepidisphaerales, together with the fungal species *Papiliotrema rajasthanensis*, *Ustilago maydis*, *Chrysosporium pseudomerdarium*, *Clonostachys intermedia*, and a member of the genus *Cercophora*.

In regards to organic farming, irrigated soils (OI) in both wheat and spelt (Table 7) had an enrichment of a bacterial species belonging to Nitrosococcaceae SZB85, in addition to the fungal species *Stachybotrys chartarum*, *Botryotrichum spirotrichum*, *Albifimbria verrucaria*, and members of Geomyces and *Curvularia*. Rainfed soils (OR) had an increase of bacterial species of Blastocatellaceae, Ilumatobacter, Isosphaeraceae, Thermomicrobiales and JG30-KF-CM45, as well as fungal

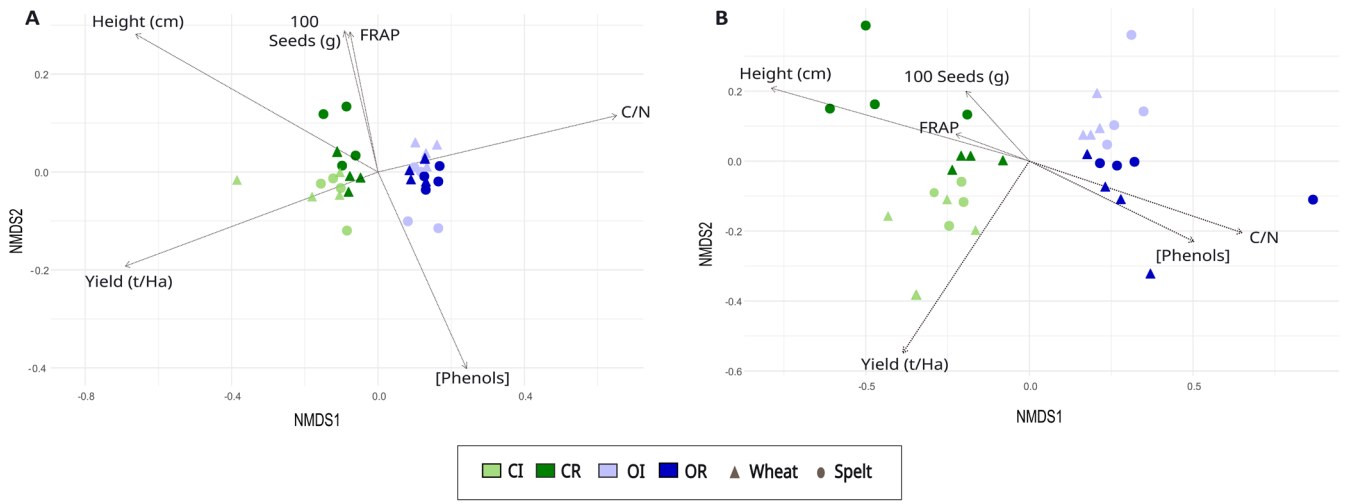



**FIGURE 5** | Non-metric multidimensional scaling (NMDS) representing the dissimilarity in soil microbiota composition of (A) bacterial and (B) fungal communities. Samples are coloured by the combination of farming practice and irrigation system (Light Green: CI, Dark Green: CR, Light Blue: OI, Dark Blue: OR) while shapes indicate the crop sample belongs to (Triangle: Wheat; Circle; Spelt). Crop performance parameters are inserted as vectors (*Height*, *Yield*, *100-grain weight*, *Phenols*, *Antioxidant capacity* and *C/N* ratio). Performance parameters are overlaid as arrows, indicating the direction and strength of correlation with the microbial community composition.

**TABLE 6** | Differentially bacterial and fungal members enriched in both crops for conventional irrigated (CI) and conventional rainfed (CR). Results based on LEfSe analysis: $p < 0.01$ and LDA > 2 for bacteria and $p < 0.025$ and LDA > 2 for fungi. The relative abundance ASV table was collapsed to species level prior statistical analysis, and the table represents the deepest taxonomic group identified to which each microorganism belongs.

| | | Wheat | | Spelt | |
|---|---|---|---|---|---|
| **Taxonomic groups** | **Treatment enriched** | **LDA** | ***p*** | **LDA** | ***p*** |
| *Pirellula* | CI (Bacteria) | 3.40 | 0.008 | 3.53 | 0.003 |
| *Solirubrobacterales* (67_14) | | 2.98 | 0.008 | 3.01 | 0.002 |
| *Pedosphaeraceae* | | 2.92 | 0.005 | 2.79 | 0.007 |
| *Conexibacter* | | 2.82 | 0.009 | 2.65 | 0.005 |
| *Terrimicrobium* | | 2.66 | 0.005 | 2.74 | 0.008 |
| *Parachlamydiaceae* | | 2.62 | 0.010 | 2.76 | 0.008 |
| *Latescibacteraceae* | | 2.48 | 0.009 | 2.50 | 0.008 |
| Gemmatimonadaceae | | 2.29 | 0.005 | 2.43 | 0.004 |
| *Claroideoglomus* | CI (Fungi) | 4.02 | 0.006 | 4.03 | 0.003 |
| *Humicola fuscoatra* | | 3.73 | 0.005 | 3.64 | 0.005 |
| *Funneliformis geosporum* | | 3.55 | 0.006 | 4.07 | 0.014 |
| *Didymella* | | 3.34 | 0.012 | 3.26 | 0.007 |
| *Ramicandelaber* | | 3.29 | 0.003 | 3.31 | 0.005 |
| *Tetracystis sarcinalis* | | 3.22 | 0.004 | 3.09 | 0.004 |
| *Scutellinia* | | 3.21 | 0.011 | 3.09 | 0.014 |
| *Cephalotrichum asperulum* | | 3.13 | 0.006 | 3.14 | 0.004 |
| *Coelastrella* | | 3.06 | 0.007 | 2.85 | 0.003 |
| *Botrytis* | | 3.05 | 0.009 | 3.13 | 0.013 |
| *Bracteacoccus* | | 3.02 | 0.008 | 3.15 | 0.006 |
| *Coniochaeta baysunika* | | 2.93 | 0.009 | 2.61 | 0.018 |
| *Diversispora* | | 2.91 | 0.024 | 3.04 | 0.013 |
| *Monilinia* | | 2.90 | 0.005 | 2.70 | 0.006 |
| *Paramyrothecium* | | 2.83 | 0.020 | 2.74 | 0.006 |
| *Malbranchea flocciformis* | | 2.73 | 0.016 | 2.85 | 0.004 |
| *Stichococcus* | | 2.29 | 0.012 | 3.01 | 0.005 |
| Geminicoccaceae | CR (Bacteria) | 3.31 | 0.007 | 2.98 | 0.005 |
| Tepidisphaerales (WD2101) | | 3.14 | 0.004 | 3.00 | 0.005 |
| *Papiliotrema rajasthanensis* | CR (Fungi) | 3.75 | 0.019 | 2.85 | 0.013 |
| *Ustilago maydis* | | 3.66 | 0.021 | 3.76 | 0.024 |
| *Cercophora* | | 3.03 | 0.004 | 3.10 | 0.005 |
| *Chrysosporium pseudomerdarium* | | 2.78 | 0.010 | 2.45 | 0.007 |
| *Clonostachys intermedia* | | 2.44 | 0.007 | 2.02 | 0.005 |
| *Lipomyces tetrasporus* | | 2.13 | 0.005 | 2.15 | 0.005 |

**TABLE 7** | Differentially bacterial and fungal members enriched in both crops for organic irrigated (OI) and organic rainfed (OR). Results based on LEfSe analysis: $p < 0.01$ and LDA > 2 for bacteria and $p < 0.025$ and LDA > 2 for fungi. The relative abundance ASV table was collapsed to species level prior statistical analysis, and the table represents the deepest taxonomic group identified to which each microorganism belongs.

| | | Wheat | | Spelt | |
|---|---|---|---|---|---|
| **Taxonomic groups** | **Treatment enriched** | **LDA** | ***p*** | **LDA** | ***p*** |
| Nitrosococcaceae SZB85 | OI (Bacteria) | 2.25 | 0.004 | 2.13 | 0.006 |
| *Stachybotrys chartarum* | OI (Fungi) | 3.92 | 0.007 | 3.80 | 0.014 |
| *Botryotrichum spirotrichum* | | 3.78 | 0.013 | 3.80 | 0.018 |
| *Albifimbria verrucaria* | | 3.49 | 0.003 | 3.36 | 0.004 |
| *Geomyces* | | 2.93 | 0.005 | 3.02 | 0.008 |
| *Lectera longa* | | 2.91 | 0.003 | 2.44 | 0.010 |
| *Curvularia* | | 2.85 | 0.006 | 2.82 | 0.004 |
| *Arthrinium* | | 2.46 | 0.016 | 2.75 | 0.006 |
| Blastocatellaceae | OR (Bacteria) | 3.60 | 0.007 | 3.62 | 0.007 |
| *Ilumatobacter* | | 3.20 | 0.008 | 3.13 | 0.009 |
| *Isosphaeraceae* | | 3.20 | 0.009 | 3.30 | 0.010 |
| JG30-KF-CM45 | | 3.08 | 0.010 | 3.04 | 0.009 |
| *Luteitalea* | | 2.81 | 0.009 | 2.95 | 0.008 |
| *Burkholderiaceae* | | 2.44 | 0.005 | 2.45 | 0.007 |
| Thermomicrobiaceae | | 2.43 | 0.004 | 2.39 | 0.004 |
| *Caldilineaceae* | | 2.32 | 0.004 | 2.14 | 0.004 |
| *Actinomycetospora* | | 2.19 | 0.006 | 2.36 | 0.004 |
| *Gibberella* | OR (Fungi) | 3.86 | 0.008 | 3.80 | 0.016 |
| *Rhizopus arrhizus* | | 3.71 | 0.007 | 3.88 | 0.014 |
| *Paraphoma radicina* | | 3.39 | 0.004 | 3.17 | 0.003 |
| *Keissleriella* | | 3.29 | 0.008 | 2.88 | 0.007 |
| *Murispora* | | 3.24 | 0.006 | 3.19 | 0.006 |
| *Alternaria chlamydosporigena* | | 2.78 | 0.005 | 2.66 | 0.003 |
| *Subulicystidium* | | 2.70 | 0.017 | 2.71 | 0.008 |
| *Talaromyces ucrainicus* | | 2.64 | 0.005 | 2.70 | 0.004 |
| *Neonectria major* | | 2.14 | 0.007 | 2.37 | 0.011 |

species *Rhizopus arrhizus* and *Paraphoma radicina*, together with members of *Gibberella*, *Keissleriella* and *Murispora* (Table 7).

## 4 | Discussion

Climate change is increasing the frequency of drought events, negatively affecting the yields of conventional crops like wheat (The Core Writing Team IPCC 2021). Therefore, it is essential to explore alternative crops that are more resilient to water-limited conditions. Spelt, an ancestral relative of wheat, has attracted attention in recent years, although contradictory findings exist regarding its drought resilience (Radzikowska et al. 2022; Kosakivska et al. 2023; Martínez-Goñi et al. 2023). Additionally, farming practices, particularly the transition from conventional to organic farming tend to promote greater soil microbial diversity (Smith et al. 2019). Soil microbial communities play a key role in enhancing plant resilience to water scarcity, particularly by improving drought tolerance in the rhizosphere (Hartman and Tringe 2019). Nevertheless, the interaction between water-limited conditions and farming practices in spelt has not been fully investigated, highlighting the need to assess its tolerance under rainfed field conditions, especially in comparison to wheat. This study seeks to address this gap of knowledge by evaluating the agronomical and physiological responses, as well as the modulation of the

soil microbial community of both crops under different farming systems and different water availability regimes. To achieve this, we assessed the growth of wheat and spelt during an unusually dry and warm year (Table 1), where the hottest and driest months coincided with the reproductive stage of wheat and spelt (Z55-92), a phase highly sensitive to water scarcity (Gray and Brady 2016).

### 4.1 | Spelt Prioritises Above-Ground Height While Wheat Focuses on Grain Production Under Irrigated Conditions

The growth of wheat and spelt was contrasting under conventional farming practices and irrigated conditions, despite their soil microbial composition being similar. In fact, results evidenced that, under irrigated conditions, spelt prioritises the growth of aerial vegetative tissues over grain production (77 cm height and 2.08 t/ha yield), whereas wheat appears to focus more on promoting grain production with less emphasis on height (47 cm height and 8.51 t/ha yield; Figure 1A,B). This difference in resource allocation between the two species highlights distinct growth strategies, with spelt investing more in above-ground height and wheat directing resources towards yield. The Green Revolution, an agrotechnological movement aimed at improving cereal yields that began in Mexico in the mid-20th century, initiated the development of semi-dwarf crops (Borojevic and Borojevic 2005; Borlaug 2007). These crops were designed to promote resource allocation to grain production rather than height promotion in the shoots, in order to obtain high-yield crops. This shift allowed for higher productivity crops in terms of yield, particularly in wheat and rice, while also improving resistance to lodging and drought stress. Thus, it was not unexpected finding that spelt allocates more resources to height, as it has not been subjected to the same intensive breeding programs as wheat.

Despite the differences in yield between the species, the seed weight of wheat was not greater than that of spelt (3.48 g per 100 grains in both cases; Figure 1C), suggesting that wheat breeding might have been effective for increasing grain quantity but not enhancing grain filling. This has also been reported in other studies, where final grain weight shows little or no variation when comparing old wheat cultivars with modern ones, their grain filling periods not being significantly different (Álvaro et al. 2008; Motzo et al. 2010; Giunta et al. 2020). Nonetheless, the higher *C/N* ratio in wheat grains (22) compared to spelt grains (16.5) suggests a greater accumulation of carbon-rich compounds relative to nitrogen (Figure 3; Ibrahim and Jaafar 2011). This implies that spelt grains may have a higher protein concentration and, consequently, superior nutritional quality, a key finding that supports the growing reputation of spelt as a healthy alternative to modern wheat. This is supported by the higher absolute nitrogen values observed in spelt (0.85 ± 0.042 g N per 100 grains) compared to wheat (0.65 ± 0.009 g N per 100 grains). Similarly, the higher proportion of phenols in wheat grains (5.47 μmol galic acid $g^{-1}$ DW; Figure 2A) in comparison with spelt grains (4.60 μmol galic acid $g^{-1}$ DW) supports the aforementioned, pointing to a greater accumulation of carbon-based compounds over nitrogen-based compounds. Overall, our findings show that modern breeding efforts have prioritised grain quantity over grain quality in wheat, which is reflected in its reduced height to allocate resources towards grain production compared to spelt. As a result, while spelt grains possess a higher nutritional quality, breeding efforts for this alternative crop must focus on increasing grain quantity to make it a suitable alternative to wheat under optimal (irrigated) conditions.

### 4.2 | Spelt Exhibits Improved Resource Allocation, Yield Stability and Antioxidant Response but Reduced Soil Microbial Diversity Under Conventional Rainfed Environments

Compared to conventional irrigated conditions, rainfed led to increased plant height in both wheat (+17.55%) and spelt (+15.62%; Figure 1A). This unexpected growth response may indicate a drought-escape strategy, where plants accelerate stem elongation to complete their life cycle before water availability further declines (Shavrukov et al. 2017). In wheat, this response was accompanied by a significant yield reduction and a decrease in grain weight (−17% yield, −12.87% grain weight; Figure 1B,C), suggesting a trade-off between growth and grain production to ensure survival. Conversely, spelt maintained stable yield and grain weight despite the increased height (Figure 1A–C), which may suggest an improved potential for better resource allocation and resilience under water-limited conditions. In fact, as a drought-tolerant variety, the spelt variety Franckenkorn has previously been characterised as the least affected by drought within a spelt panel, exhibiting an increased accumulation of antioxidant molecules (Radzikowska et al. 2022; Martínez-Goñi et al. 2023). In our results, a rise in antioxidant capacity in spelt was also observed (+12.93%; Figure 2B), but this was not the case in wheat, suggesting a greater ability to mitigate oxidative damage under drought stress in spelt. The enhanced antioxidant response may have provided photoprotective mechanisms, supporting the normal functioning of photosynthetic processes and ultimately contributing to stable grain production despite adverse conditions. This is also supported by the delayed senescence in spelt, which exhibited a notably longer period of greenness under these conditions (Figure S1), as the accumulation of antioxidant molecules and osmolytes has previously been shown to be a key drought-adaptive trait that enables drought-tolerant species to delay leaf senescence and maintain greenness (Fang and Xiong 2015). This prolonged greenness supported an extended grain-filling period, allowing spelt to sustain both grain production and grain weight under water scarcity. Altogether these results highlight spelt possessing more effective mechanisms to mitigate limited-water conditions and maintain productivity. Nonetheless, it is important to note that, despite spelt exhibiting advantageous traits to cope with water limitation, wheat preserved a grain production that was 229% higher (7.06 t/ha in wheat vs. 2.15 t/ha; Figure 1B). Therefore, breeding efforts for spelt should not solely focus on increasing its productivity but rather aim to enhance yield while preserving its drought resilient traits.

Given the fundamental role of belowground ecosystems in plant development, it was essential to analyse how both crops' performance and health could be affected by variations in soil microbial communities, underscoring the importance of the continuous feedback loop between the soil microbiome and plant host (Bauer et al. 2017). The present work shows that,

under conventional farming, water limitation reduced the alpha diversity of bacterial and fungal communities in the soil in spelt but not in wheat (Figure 4A,B), suggesting that the spelt-associated microbiota is more sensitive to water scarcity. This increased sensitivity may be related to the ability of spelt's root system to engage more effectively with the soil microbiota under irrigated conditions, potentially through the exudation of specific compounds, as observed in other species (Williams and de Vries 2020). Conversely, under rainfed, spelt may reallocate resources by, for instance, reducing the investment of elemental compounds in root exudation thereby diminishing bacterial communities, while prioritising the synthesis of antioxidant compounds to enhance photoprotection and mitigate oxidative damage. Besides, the reduction in bacterial diversity and the increased dominance of specific bacterial taxa under water-limited conditions may not necessarily be detrimental. It is plausible that spelt could be selectively promoting a core group of beneficial drought-tolerant bacterial communities through its root exudates, favouring those that provide advantages for coping with limited-water conditions (Williams and de Vries 2020; Gu et al. 2024). In the same manner, the decrease in the Shannon Index of fungal communities in spelt under water-limited conditions in the conventional farming (Figure 4B2) led us to hypothesise that drought-tolerant fungal taxa might be increasing.

This interaction between each crop species and its microbial communities under different water regimes suggests a dynamic balance, where shifts in microbial diversity may represent adaptive strategies to support plant health and stress resilience. To further investigate this phenomenon, we analysed which microbial taxa, shared by both crops, were key under each condition, aiming to identify soil-specific biomarkers associated with distinct environmental conditions, regardless of the crop type. Within the bacterial community, a member of Geminicoccaceae was enriched under conventional rainfed soils. This family includes certain species known for their salt tolerance, which is consistent with the fact that several defence mechanisms present in certain bacteria, such as plant growth-promoting rhizobacteria conferring stress tolerance to plants, are commonly shared in mitigating the effects of drought (García et al. 2017). These mechanisms may potentially help both crops in our study cope with the abiotic challenge they encounter. In addition, under CR conditions, a member of *Conexibacter* was reduced. This genus is recognised as a beneficial bacterium potentially recruited by a wide range of cereals like maize to participate in the phosphorus cycle and promote rapid plant growth (Deng et al. 2021), suggesting that such functional interactions may be compromised under conventional rainfed environments.

In fungal community, under CR conditions, composition analysis revealed that the fungus *Chrysosporium pseudomerdarium* was enriched in both crops (Table 6), a species known to promote plant growth and development under drought stress (Hamayun et al. 2009). However, an enrichment of the pathogenic fungi *Ustilago maydis* was also observed, which so far, has been seen to affect maize, another cereal crop Notably, these type of pathogens tend to thrive under warm and dry conditions (Boland et al. 2004), which aligns with the environmental conditions associated with our CR treatment. In particular, *U. maydis* outbreaks are known to intensify under drought followed by heatwaves (Merkevičiūte-Venslovė et al. 2022), suggesting that such stresses may facilitate its spread in field settings. These findings are consistent with previous studies showing that high temperatures and drought during specific stages of fungal development can significantly influence the prevalence and severity of smut diseases (Venslovas et al. 2023). On the contrary, in the conventional irrigated soils, there was an enrichment of a member of *Claroideoglomus* in both crops, which is known for establishing symbiotic relationships with plants and has been associated with drought resistance, increased plant height, enhanced biomass accumulation in both shoots and roots and improved nutrient uptake (Shao et al. 2018; Wu et al. 2024). *Humicola fuscoatra*, a biofertiliser microorganism with compost-enriching activity (Salimi and Hamedi 2021), and *Funneliformis geosporum*, an arbuscular mycorrhizal fungus (AMF) that, together with other AMFs, helps common wheat plants maintain the structure and function of PSI and PSII under drought conditions (Mathur et al. 2019), were also enriched. It might seem intuitive that the microorganisms mentioned above, known to support plants tolerance to water stress, would be enriched under rainfed environments. However, irrigation can promote greater biomass production and root exudation, creating a favourable environment for the proliferation of AMF such as *F. geosporum*. Conversely, under water stress, carbon limitation could restrict the plants to maintain such symbiotic relationships, as plants may tend to prioritise intrinsic survival mechanisms, such as antioxidant metabolism and osmotic adjustment, over sustaining energy-intensive associations (Jacoby et al. 2017; Basu et al. 2018; Haghpanah et al. 2024).

All these results suggest that soil stress caused by water limitation may favour the emergence of opportunistic pathogens, while simultaneously prompting the plant to recruit microorganisms that perform beneficial functions under drought conditions, even when optimal conditions for exudate production are not available. In addition, these findings highlight the complex interaction between plant traits and soil microbial communities under contrasting water regimes, since while spelt exhibited notable physiological advantages under water-limited conditions, its soil microbial diversity also appeared more sensitive, suggesting a possible link underlying this phenomenon. Additionally, microbial biomarkers related to water stress shared by both crops were identified, highlighting a soil response that is both host-specific and general. All of this underscores the need to manage soil health alongside crop traits to achieve optimal crop yields in a climate change scenario.

### 4.3 | Organic Practices Reduce Grain Yield and Quality, and Modulate Soil Microbial Diversity and Structure in Wheat and Spelt

Organic farming practices had a negative impact on the agronomic traits of both wheat and spelt irrespective of the water treatment, likely due to insufficient nutrient availability for their optimal growth and development. Previous studies have reported that organic practices often result in reduced biomass accumulation and, more importantly, lower yields in various crop species, including wheat (Döring and Neuhoff 2021). As a matter of fact, previous research has estimated yield losses in cereal crops, including wheat, of between 60% to 73% if agriculture were to transition from conventional to organic practices

(Smith et al. 2018; Döring and Neuhoff 2021). In our study, grain yield in wheat was decreased by 80%–85%, while in spelt it was decreased by 60%–80% (Figure 1B). Specifically, the average wheat yield values in our results were 7.06–8.51 t/ha, which were reduced to 1.10–1.90 t/ha under organic practices. These decreases in yield are likely occurring due to the lower nutrient availability in organic soils, which, regardless of how naturally nutrient-rich they may be, are not capable of competing with the higher nutrient concentrations provided by synthetic fertilisers (see Section 2: Materials and Methods and Table 3). In 2022, global wheat production in the top 10 producer countries ranged from 2.85 to 7.60 t/ha, with an average value of 4.32 t/ha (FAOSTAT 2025). The wheat yields under organic farming practices in our study (1.90 t/ha) are significantly lower than these global averages. This finding reinforces the notion that a large-scale widespread adoption of organic practices could create considerable risk to global wheat production, potentially threatening global food supply and increasing food insecurity. Additionally, despite comparable grain weights between conventional and organic practices (Figure 1C), the higher *C/N* ratio values in conventional rather than in organic (+30.67% in wheat and +36.92% in spelt) suggest a reduced protein content in the grains of organic farming (Figure 3). This is likely attributed to the lower nitrogen availability in organic soils, a finding consistent with previous reports on wheat (Casagrande et al. 2009; Grausgruber et al. 2024). Therefore, organic practices not only had a negative impact on yield but also on the quality of the produced grains. Interestingly, spelt maintained its ability to increase antioxidant capacity in its grains when exposed to water limitation under organic practices. This response could be linked to the observed increase in the *C/N* ratio in the grains, as the plant may prioritise carbon accumulation and antioxidant production while limiting nitrogen uptake under rainfed. This finding suggests that spelt has a robust physiological mechanism for coping with limited-water availability, enabling it to reallocate resources towards antioxidant production not only under limited-water availability but also when nutrients are scarce. This trait likely explains its superior adaptability to suboptimal growing conditions compared with modern high-yield wheat varieties, which have been bred mainly for performance in conventionally irrigated, high-input systems.

Seeking to understand the role of soil microbiota in the observed changes in aboveground parameters, bacterial and fungal diversities in the soil were found to be highest in conventional soils compared to organic ones for both crops, particularly under irrigated condition (Figure 4). In fact, wheat exhibited 23.70% and 19.47% less ASV in organic soils for bacterial and fungal communities, whereas in spelt those values were 21.48% and 12.46% lower. This finding was initially unexpected, as prior studies have generally reported enhanced microbial diversity under organic agricultural practices compared to conventional systems (Bebber and Richards 2022). The lower microbial diversity in the organic soils, despite a history of organic management and the presence of a Crotalaria cover crop prior to the experiment, could be a result of not supplementing the soils under study with organic fertilisers. While the Crotalaria cover crop likely provided some benefit and the soils were classified as nutrient-rich, organic fertilisers, such as compost or manure, are crucial for directly introducing a variety of beneficial microbes and providing additional nutrients that can stimulate microbial growth and enhance diversity (Wang et al. 2023). Without this external input, the organic soils may not have had the necessary resources to foster their diversity. Our results, therefore, imply that, in the absence of external organic inputs, the microbial diversity in long-term organic soils may not reach the levels typically associated with organic farming systems. This highlights the importance of organic fertilisers in actively promoting a diverse microbial community. In contrast, the conventional soils, which were supplemented with readily available NPK fertilisers, likely created an environment that promoted a rapid, short-term increase in the population of microbes that thrive on these nutrient inputs. Additionally, the overall lower plant growth in the organic plots (Figure 1A), likely due to insufficient nutrient availability, would have resulted in a reduced quantity of root exudates, also leading to limitations in the development of a diverse microbial community. Thus, the absence of an organic fertiliser input might have limited microbial diversity not only by failing to introduce a variety of microorganisms and nutrients, but also by indirectly limiting microbial development due to the limitation of plant growth and root exudates. Despite this idiosyncrasy in the farming practices studied, and focusing more on composition than diversity, the analysis of the belowground microbial ecosystem revealed that farming practice was the main factor driving differences in microbial community composition, while the irrigation system played a secondary role (Figure 5). This may be because farming practices directly alter soil nutrient availability, organic matter inputs, and physical disturbance, all of which have immediate impacts on microbial habitats and resource distribution. In contrast, irrigation affects soil moisture dynamics, influencing microbial activity without necessarily causing major shifts in the main taxonomic groups.

Although the irrigation system was a secondary factor in community composition, it played an important role in microbial diversity when comparing organic and conventional practices. Interestingly, similar microbial diversities were observed in conventional and organic soils under water-limited conditions (Figure 4A,B), which may be explained by moisture-dependent microbial activity. In rainfed (low-moisture) soils, limited-water availability likely induces physiological dormancy in microbial communities, reducing overall metabolic activity and potentially reducing microbial growth (Stark and Firestone 1995). Our results indicate that, under these conditions, water availability likely became the dominant limiting factor for microbial activity in both farming practices, effectively mitigating the nutrient advantage present in the conventional soils.

In spite of the lower overall microbial diversity, organic farming promoted an enrichment of soil bacterial microorganisms involved in nitrogen cycling and organic matter degradation (Table 7). The increased presence of Nitrosococcaceae SZB85 indicates enhanced nitrification processes, as these genera include ammonia-oxidising bacteria that play a crucial role in the nitrogen cycle by oxidising ammonia to nitrite (Flood et al. 2021; Zhang et al. 2022). The increase in these microorganisms aligns with the observed shift towards nitrogen-scavenging communities under organic practices, where limited fertilisation inputs drive microbial recruitment for nutrient acquisition (Behr et al. 2023). Burkholderiaceae has been previously related to improved root growth in organic soils (Liu

et al. 2021; dos Santos et al. 2022). Similarly, Thermomicrobiaceae has also been recognised as a family associated with the nitrifying microbial fraction (Qu et al. 2022), and has been reported to contribute to the degradation of organic matter, playing a role in nutrient cycling. In addition, Verrucomicrobiaceae, known for its significant role in organic matter degradation and nutrient cycling, was also enriched (Orellana et al. 2022). Finally, the genus *Actinomycetospora*, associated with key processes in carbon and nitrogen cycling (Jiang et al. 2008), was observed also to be more abundant in organic soils. However, despite the enrichment of beneficial microbial communities, this was not translated into a favourable agronomic outcome for wheat or spelt (yield reductions 57%–85%). As a result, while overall microbial diversity was decreased in the organic plots, the system supported an enriched bacterial community of taxa related to nutrient cycling. However, the reliance on the slower, microbial-driven processes of nutrient release from existing soil organic matter was insufficient to compete with the high yields from the readily available synthetic nutrients in conventional plots. The observed enrichment of the Verrucomicrobiaceae family further supports this interpretation, as this family has been acknowledged as an indicator of poor soil physicochemical properties and low soil fertility (Navarrete et al. 2015; Solórzano-Acosta et al. 2025). Therefore, our results suggest that while organic farming practices successfully promote bacterial groups associated with nutrient-rich soils, the absence of an external organic nutrient input was insufficient to meet the high nutrient demands of wheat and spelt, highlighting a critical trade-off between soil health and short-term crop productivity.

In fungal communities, interestingly, *Lectera longa*, previously identified as a potential pathogen (Ren et al. 2023), exhibited limited presence in conventional soils but had a significantly higher relative abundance in irrigated organic soils in both crop species (Tables 6, 7). Although its presence may increase the risk of plant infection, there are no known reports of this species negatively affecting wheat or spelt. It is plausible these fungi inhibit the growth of other pathogenic groups, thus benefiting the crops, or negatively impact the growth of other grasses to promote the growth of wheat and spelt. Our results contradict previous findings, which reported an increase in *L. longa* associated with higher nitrogen fertilisation (Jacquiod et al. 2022; Ren et al. 2023). We also observed the highest relative abundance of *Paraphoma radicina* under organic rainfed environments in both species. This species has been recognised as a dark septate endophyte, and its inoculation in wheat led to increases in plant height, leaf growth, chlorophyll content, and photosynthetic rate, as well as a decrease in intercellular carbon dioxide, which alleviates the damage caused to photosynthetic processes by drought (Huertas et al. 2024). Interestingly, *P. radicina* has demonstrated the ability to colonise wheat under varying water conditions (Sari Lubis et al. 2025), with reported positive effects on plant biomass, vegetative growth, and physiological parameters during drought. Furthermore, while it is considered to be a pathogenic fungus for species like *Medicago sativa* and *Prunus cerasus*, it is not known to be pathogenic for cereals (Dang and Li 2022). Therefore, its increase in both crops, similar to *L. longa*, may help benefit them by limiting the growth of other pathogenic fungi or by promoting spelt and wheat competition over other grasses. Additionally, under organic rainfed environments, the enrichment of the fungus *Rhizopus arrhizus* may have helped promote antioxidant activity in spelt, as previously reported to occur in maize under drought stress (Taha et al. 2025).

In summary, conventional practices supported higher overall microbial diversity, likely due to the readily available nutrients provided by synthetic fertilisers. Although organic soils exhibited lower microbial diversity, they showed enrichment of beneficial microbial taxa involved in nutrient cycling, suggesting a compositional shift. The irrigation system influenced microbial diversity and activity, especially under organic management, but farming practice remained the dominant factor shaping microbial community composition. These results emphasise the need for integrated management strategies that combine sustainable agricultural inputs and practices to enhance both soil microbial health and crop productivity.

## 5 | Conclusions

Our study demonstrates that wheat (*Triticum aestivum*) and spelt (*Triticum spelta*) exhibit distinct responses to irrigation systems and farming practices, with significant implications for agronomic performance, physiological traits, and soil microbial communities. Under irrigated conditions, wheat allocated resources primarily towards grain production, while spelt invested more in height promotion. However, under conventional rainfed environments, spelt exhibited superior resilience compared to wheat, maintaining stable yields (2.15 t/ha) and grain weight (3.48 g). This resilience is likely attributed to the enhanced antioxidant capacity (+10.3%) of spelt. In addition, under organic farming practices soilborne microbiota experienced significant compositional shifts in both crops, with an enrichment of bacterial groups involved in nutrient cycling and organic matter degradation. This was likely explained by a compensatory response to lower nitrogen availability under the particular conditions of the organic soils studied here that did not receive additional organic input. However, this was not sufficient to prevent nitrogen deficiencies under organic practices, resulting in reduced yields in both crops (77%–85% reduction for wheat and 57%–85% for spelt). We found spelt grains to consistently exhibit lower *C/N* ratios, indicating greater protein content. In addition, spelt was capable of preserving grain quality parameters, including antioxidant capacity and phenols, suggesting that water scarcity does not severely compromise its nutritional value. Water-limited conditions in conventional soils promoted the proliferation of potentially pathogenic fungi such as *Ustilago maydis*. However, simultaneously both crops recruited beneficial microorganisms like *Chrysosporium pseudomerdarium* in CR and *Rhizopus arrhizus* and *Paraphoma radicina* in OR. These results provide critical insights for breeding programs and agricultural strategies aimed at enhancing food security in water-limited regions. The drought-tolerance traits of spelt, combined with its capacity to maintain grain quality under stress, positions it as a promising candidate for breeding initiatives focused on yield improvement without compromising its drought resilience.

### Author Contributions

X.S.M.-G., J.M.-A. and U.P.-L. were responsible for the initial conceptualisation. X.S.M.-G. and J.M.-A. developed the methodology and conducted the investigation. A.C. and I.Z. handled the software resources

and technical implementation. X.S.M.-G. and A.C. performed data curation and formal analysis/validation of the results. U.P.-L. was responsible for supervision, project administration and securing resources. X.S.M.-G., J.M.-A. and U.P.-L. acquired funding for the project. X.S.M.-G., A.C. and I.Z. were involved in data visualisation. Finally, X.S.M.-G., A.C., I.Z. and U.P.-L. contributed to both the writing – original draft and writing – review & editing of the manuscript.


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### Conflicts of Interest

The authors declare no conflicts of interest.

### Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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**Supporting Information**

Additional supporting information can be found online in the Supporting Information section. **Figure S1:** Results of RGB camera-derived vegetative indices over time: (A) Normalised Green/Red Difference Index (NGRDIveg), (B) Triangular Greenness Index (TGIveg), (C) Green Area (GA), (D) Greener Green Area (GGA) and (E) Crop Senescence Index (CSI). Results for wheat (circles) are represented as follows: conventional irrigated (CI, light red), conventional rainfed (CR, dark red), organic irrigated (OI, light green) and organic rainfed (OR, dark green). Results for spelt (squares) are represented as follows: conventional irrigated (CI, light blue), conventional rainfed (CR, dark blue), organic irrigated (OI, light purple) and organic rainfed (OR, dark purple). DAS indicate days after sowing. **Figure S2:** Cladogram plotted from LEFSE analysis highlighting the bacterial groups whose abundances are significantly enriched on each condition for (A) Wheat and (B) Spelt. Conditions: Conventional irrigated (CI), conventional rainfed (CR), organic irrigated (OI) and organic rainfed (OR). The ASV relative abundance table was collapsed to species level prior statistical analysis and the groups significantly enriched were used for plotting the cladogram (LDA $>2$, $p<0.05$). Branches show evolutionary relationships, while labels are represented up to family. **Figure S3:** Cladogram plotted from LEFSE analysis highlighting the fungal groups whose abundances are significantly enriched on each treatment for (A) Wheat and (B) Spelt. Treatments: conventional irrigated (CI), conventional rainfed (CR), organic irrigated (OI) and organic rainfed (OR). The ASV relative abundance table was collapsed to species level prior statistical analysis and the groups significantly enriched (LDA $>2$) were used for plotting the cladogram. Branches show evolutionary relationships, while labels are represented up to family or genus. **Table S1:** Daily average air temperature (T), relative humidity (H) and total precipitation (Rain) in the region where wheat and spelt were grown for the period of the experiment.