



## Article

# Establishing the Effects of Climate and Soil on the Nutritional Composition of an Array of Faba Bean Varieties Grown in Two Different Zones of Andalusia, Spain

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## Abstract

Legumes contribute to sustainable agriculture by reducing fertilizer use, enhancing nitrogen fixation, and with high species diversity (~20,000 species). Spain is a leading EU producer, yielding up to 30,000 tons of different legume varieties annually. The Mediterranean climate, particularly in regions like Andalusia, is under increasing pressure from climate change, with extreme temperature variations and drought becoming more frequent. While these changes may jeopardize crop yields, limited information is available on their effects on the nutritional profile of legumes. From 2017 to 2019, six faba bean (*Vicia faba*) varieties were monitored in two climatically distinct areas of Andalusia to assess the impact of temperature (T) and rainfall (R) on key nutrients and bioactive compounds, including protein, minerals (K, Ca, Mg, Zn, P, Fe, Mn, B), total polyphenol content (TPC), tannins (TA), and saponins (S). Spearman correlations showed that higher T negatively impacted TPC ( $r = -0.40$ ) and Mg ( $r = -0.33$ ), while positively influencing Zn ( $r = 0.27$ ) and Ca ( $r = 0.22$ ). Rainfall increased TPC and Mg but reduced TA, Zn, and Ca. Canonical correspondence analysis (CCA) and PERMANOVA ( $p < 0.001$ ) confirmed T, R, and yield as significant factors. These insights support breeding strategies for climate-adapted, nutrient-rich faba beans and the development of more resilient food systems.

**Keywords:** legumes; faba bean; plant protein; climate change; Andalusia



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## 1. Introduction

Legumes are valued for their nutritional quality and environmental benefits, particularly their ability to fix atmospheric nitrogen and improve soil fertility [1,2].

Among them, faba bean (*Vicia faba*) is an important annual temperate grain legume, cultivated across nearly three million hectares worldwide, with an annual production of 7.8 million tons [3]. After decades of decline, its cultivation is resurging due to the growing demand for sustainable, plant-based protein sources [4,5].

Faba beans are nutrient-dense foods, rich in protein, dietary fiber, B vitamins, and minerals such as magnesium (Mg), iron (Fe), zinc (Zn), potassium (K), as well as antioxidants including tannins (TA), carotenoids (CARs), and phenolic acids (PA). They also contain

phytochemicals with antioxidant activity, contributing to their potential role in addressing dietary deficiencies in protein, fiber, and micronutrients. Regular consumption has been shown to enhance the nutrient density of human diets [5,6].

In Europe, faba bean production reached 1,850,516 tons of dry beans in 2023, with Spain contributing around 27,570 tons annually [7]. There are currently more than 830 registered cultivars of faba beans in the European Union (EU), a diversity that could be further enhanced through the characterization and use of over 26,000 accessions stored in gene banks worldwide [8].

Spanish cultivation benefits from the country's mild Mediterranean climate [9]. However, soil conditions vary greatly across Spanish territories due to differences in climate, land use and overall geology, resulting in soils with low organic carbon content (<0.5–2%) in arid areas like Andalusia. Research has shown that soils with higher organic matter content can enhance crop nutrient levels [10], while soil properties such as pH, microbial activity, and redox status can influence micronutrient uptake in plants [11]. However, the impact of soil and climatic variability on the nutritional composition of faba beans in Spain remains insufficiently documented. In Andalusia, the Mediterranean climate is characterized by average temperatures ranging from 9 °C in January to 36 °C in August, and annual rainfall between 400 and 600 mm [12]. Studies indicate that elevated temperatures can negatively affect plant roots, directly influencing crop yield and traits [13]. Similarly, offseason rainfall or unexpected drought periods can affect crop yield if they occur during critical growth stages [14]. Adverse climatic conditions are expected to become more frequent in the Mediterranean region, raising concerns about the true impact of temperature and rainfall on legume crops.

To ensure the sustainability of legume cultivation in Europe, it is crucial to identify the most suitable regions for production—areas where high yields can be obtained and where varieties can adapt to local climate and soil conditions.

This study evaluates the influence of environmental conditions on the nutritional profile of faba bean accessions grown in two Andalusian locations across two seasons. By comparing six varieties and applying different statistical analyses such as principal component analyses (PCA), the study aims to identify key factors affecting nutrient composition. These findings are expected to provide valuable insights into crop management and the agri-food sector, supporting the broader integration of legumes into sustainable European food systems.

## 2. Materials and Methods

### 2.1. Study Site

Field experiments were conducted in Andalusia, Spain, along two harvesting seasons from December to June: Season 1 (S1), 2017–2018, and Season 2 (S2), 2018–2019. These took place at the experimental fields of the Spanish National Research Council (CSIC) in Córdoba (L1, (37.8893° N, 4.7793° W)), and at a commercial farm at Almodóvar del Río (L2, (37.8132° N, 5.0146° W)). Table 1 shows the average climatic and soil conditions of this study.

**Table 1.** Average climatic and soil conditions during the trial period 2017–2019.

|                              | Location 1: Córdoba              |                                  | Location 2: Almodóvar del Río    |                                  |
|------------------------------|----------------------------------|----------------------------------|----------------------------------|----------------------------------|
|                              | S1 (2017–2018)<br>Avg. Tmax/Tmin | S2 (2018–2019)<br>Avg. Tmax/Tmin | S1 (2017–2018)<br>Avg. Tmax/Tmin | S2 (2018–2019)<br>Avg. Tmax/Tmin |
| Temperature °C               | 20.2/7.3                         | 23.8/8.6                         | 21.5/8.2                         | 23.3/8.3                         |
| Rainfall (mm)                | 405                              | 218                              | 490                              | 268                              |
| Grain yield<br>(Avg. per ha) | 3672.38                          | 3613.25                          | 3732.27                          | 3695.94                          |
| Type of soil                 | Vertisol                         |                                  | Fluvisol                         |                                  |
| Soil pH                      | 7–7.8                            |                                  | 8–8.3                            |                                  |

## 2.2. Sample Type

Six faba bean accessions were selected to conduct the field trial. Two advanced breeding lines developed within the CSIC/IFAPA breeding programs (Navio6 and Quijote), and four commercial cultivars (Omeya, Arrechana, Joya, and Prothabon), originating from local breeding programs for adaptation to Mediterranean climates. This combination was chosen to represent both advanced breeding materials of scientific interest and locally relevant cultivars, allowing for comparison between experimental lines and widely adopted accessions in the region. Table 2, adapted from [15], provides a detailed description of these accessions. All accessions belong to the type *Vicia faba* var. *minor*, a small-seeded variety characterized by the typical flower pigmentation of this type (predominantly white with some black spots) [4]. This terminology is used to distinguish standard pigmentation from color mutants or unusual variants [16]. Field trials were conducted using a randomized complete block design with three replications. Each experimental unit consisted of a 1.2 m × 5 m plot with a planting density of 60 plants m<sup>-2</sup>. A basal application of NPK 15-15-15 fertilizer (nitreNe®, Tarazona Agrosolutions, Valencia, Spain) was applied at a rate of 300 kg ha<sup>-1</sup> across all study locations. The pre-emergence herbicide pendimethalin (36%) (Most Micro HL, Sipcam Iberia, Valencia, Spain) was applied uniformly, and no fungicide treatments were administered. Sowing was performed in mid-December each season, in accordance with local agronomic practices. Precocity was evaluated weekly by recording the date when 50% of the plants had formed their first pods. Harvest took place between late May and mid-June, depending on genotype and environmental conditions. After threshing, grain yields were recorded. From the harvested seeds, three replicates were collected by accession, location, and season. Each replicate consisted of a bulk sample of seeds from multiple plants, which were subsequently used for nutritional analysis.

**Table 2.** Faba bean accessions used in this field trial.

| Accession | Type       | Flower Color | Origin   | Reference |
|-----------|------------|--------------|--|-----------|
| Navio6    | Minor type | normal       | Advanced breeding line derived from Tunisian XBJ90.03-16-1-1-1       | [8]       |
| Prothabon | Minor type | normal       | Minor type, commercial variety                                       | [17]      |
| Omeya     | Minor type | normal       | Minor type, selected from Baraca × VF1273 a sister line of cv. Joya  | [17]      |
| Arrechana | Minor type | normal       | Minor type, selected from 135  | [17]      |
| Joya      | Minor type | normal       | Minor type, selected from Baraca × VF1273 a sister line of cv. Omeya | [17]      |
| Quijote   | Minor type | normal       | Advanced breeding line derived from Tunisian XBJ90.04-6-2-1-1        | [8]       |

## 2.3. Nutritional Analysis

This study included 72 bean samples (n = 72), all of which were pulverized into flour using an industrial mill (Cyclone mill twister, RETSCH Technology, Haan, Germany) and subsequently analyzed for their nutritional characteristics using the procedures described below. Protein concentration (PC) was measured using the Bradford method [18], employing the Pierce Coomassie Plus Assay Kit (Thermo Fisher Scientific, Waltham, MA,

USA). The manufacturer's protocol was adapted for 96-well microplates by adding 5  $\mu\text{L}$  of sample extract to 280  $\mu\text{L}$  of Coomassie Plus Reagent. Total polyphenol content (TPC) was determined following the microplate-adapted procedure described in [19].

The mineral composition of grain samples was analyzed using inductively coupled plasma optical emission spectrometry (ICP-OES). Each 500 mg grain sample was combined with 10 mL of 65% nitric acid in Teflon reaction vessels and digested in a microwave system (Microwave Digestion System MARS 5, CEM Corporation, Matthews, NC, USA) following the manufacturer's guidelines. After digestion, the solutions were diluted with ultrapure water to a final volume of 50 mL, and the concentrations of K, P, Mg, Ca, Fe, Zn, Mn, and B were determined using the ICP-OES Optima 7000 DV (PerkinElmer, Shelton, CT, USA). Saponins (S) and tannins (TA) were quantified using an adapted method described in [20].

#### 2.4. Statistical Analysis

Correlation analysis and pairwise comparisons were conducted to assess the influence of environmental conditions and grain yield (GY) on the nutritional composition of faba beans at the two study locations. Spearman correlations were applied to examine relationships between nutritional components and environmental factors (temperature, rainfall, pH). Moderate correlation coefficients (CC;  $r = 0.3\text{--}0.7$ ), whether positive or negative, were further explored by visualizing faba bean nutritional composition as boxplots across different temperature and rainfall conditions. Additionally, a canonical correspondence analysis (CCA) was performed to evaluate the impact of distinct environmental conditions on specific faba bean accessions.

All statistical analysis and data visualization were performed in RStudio (V 4.4.2). Correlation analysis was conducted using the R package 'stats' (V 4.6.0) [21], applying the Spearman method, and visualized with the 'corrplot' package (V 0.92) [22]. Boxplots of nutritional components with moderate correlation coefficients were produced using the 'ggplot2' package (V 3.5.2) [23]. Statistical differences were assigned using the pairwise Wilcoxon signed-rank test from the 'stats' package.

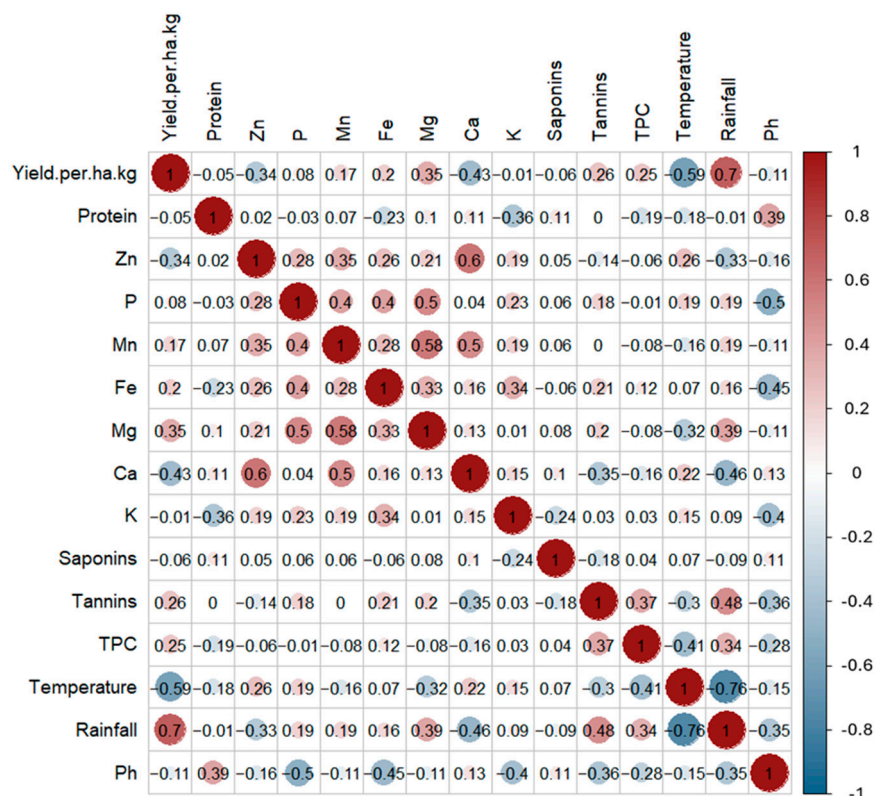
CCA was performed using the 'vegan' package in R (V 2.7-1) [24], and statistical significance was validated using PERMANOVA from the 'stats' package. The significance level was set at 5% ( $p\text{-value} < 0.05$ ). CCA results were graphically represented in a biplot using the 'ggplot2' package.

### 3. Results

#### 3.1. Environmental Influence on Nutritional Traits: Correlation Patterns

The nutritional composition of the faba bean accessions was determined using analytical methods and examined for associations with environmental parameters through Spearman correlation analysis (Figure 1). A moderate negative correlation ( $r = -0.4$ ) was observed between total polyphenol content and temperature, suggesting that higher temperatures are associated with reduced polyphenol levels. A similar trend was found for magnesium, which showed a moderate negative correlation with temperature ( $r = -0.33$ ). In contrast, moderate positive correlations were observed between temperature and tannins ( $r = 0.37$ ), zinc ( $r = 0.27$ ), and calcium ( $r = 0.22$ ), indicating that nutrient concentrations tended to increase with rising temperature.

Regarding rainfall, Spearman correlation revealed moderate negative association with tannins ( $r = -0.28$ ), zinc ( $r = -0.34$ ), and calcium ( $r = -0.46$ ), suggesting decreased nutrient content under higher rainfall conditions. Conversely, rainfall showed moderate positive correlations with total polyphenol content ( $r = 0.32$ ) and magnesium ( $r = 0.4$ ), indicating increased nutrient uptake from plants under wetter conditions.



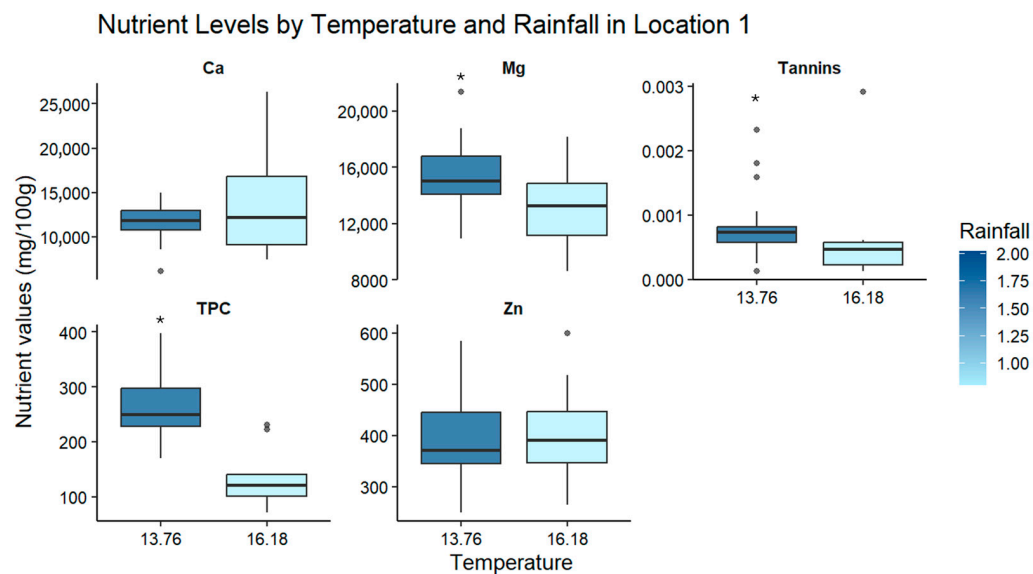
**Figure 1.** Spearman Correlation matrix showing associations among environmental factors, grain yield per ha, nutrient content, and secondary metabolites. Spearman correlation matrix; Yield.per.ha.kg-Yield as kilograms per hectare; Protein; Zn-Zinc; P-Phosphorus; Mn-Manganese; Fe-Iron; Mg-Magnesium; Ca-Calcium; K-Potassium; Saponins; Tannins; TPC-Total polyphenol content; Temperature; Rainfall (R); and pH-Potential of hydrogen.

The correlation matrix (Figure 1) also revealed moderate to strong relationships among minerals, as well as notable associations between temperature and/or rainfall and both total polyphenol content and tannin levels. These correlations provide insight into the adaptive responses of faba bean to environmental variability, as reflected in their nutritional composition. Grain yield displayed a strong positive correlation with rainfall ( $r = 0.7$ ) and a moderate negative correlation with temperature ( $r = -0.59$ ). Yield also showed weak positive correlations with magnesium, total polyphenol content, tannins, and iron ( $r = 0.20-0.35$ ), and moderate negative correlations with zinc ( $r = -0.34$ ) and calcium ( $r = -0.43$ ).

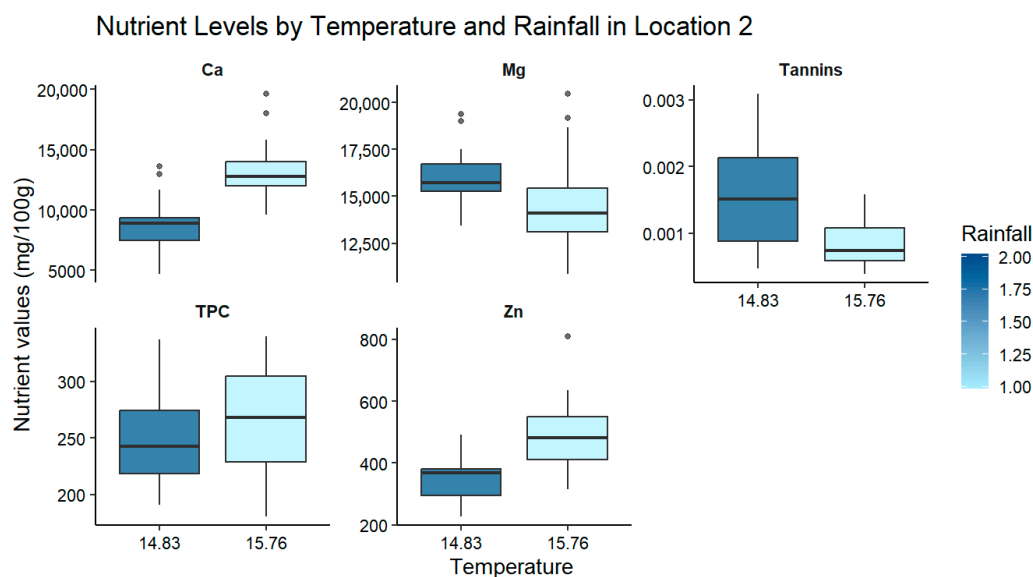
### 3.2. Exploring Nutritional Differences Across Sites and Conditions

The levels of nutritional components were visualized as boxplots across temperature ranges, with rainfall levels indicated by boxplot colors (Figures 2 and 3). These plots emphasize faba bean nutritional traits most influenced by temperature and rainfall. Detailed statistical results corresponding to the boxplots are provided in the Supplementary Materials section (Tables S1 and S2).

The boxplots (Figures 2 and 3) highlight a significant ( $p < 0.05$ ) difference in nutrient uptake in faba beans under different environmental conditions, which aligns with the correlation trend described above. At Location 1 (Figure 2), significantly higher concentrations ( $p < 0.05$ ) of total polyphenol, tannins, and magnesium contents were observed in plants exposed to higher temperature and lower rainfall. In contrast, Location 2 (Figure 3) did not exhibit statistically significant differences in nutrient concentrations.



**Figure 2.** Pairwise Wilcoxon test results comparing nutrient concentrations across temperature and rainfall levels in Location 1. \*—Statistically significant difference ( $p$ -value < 0.05) obtained by the Wilcoxon signed-rank test. Rainfall levels are reported using a color gradient where low rainfall is light blue and high rainfall is dark blue. Outliers are reported as grey dots.



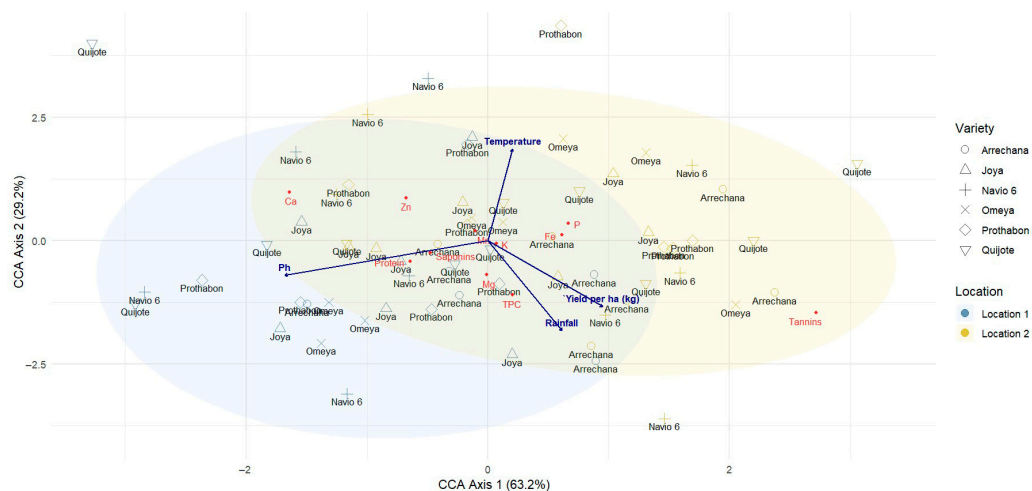
**Figure 3.** Pairwise Wilcoxon test results comparing nutrient concentrations across temperature and rainfall levels in Location 2. Rainfall levels are reported using a color gradient where low rainfall is light blue and high rainfall is dark blue. Outliers are reported as grey dots.

### 3.3. Multivariate Relationships Between Climate Factors and Faba Bean Nutrient Composition

This analysis was performed to quantify and visualize the impact of environmental gradients on plant nutritional composition, identifying key influencing factors and group accessions with similar traits under comparable conditions (Figure 4). The CCA plot displays faba bean varieties as points, distinguished by different shapes and labeled with their corresponding names, with red circles representing nutritional components and arrows denoting environmental variables (temperature and rainfall).

The results support the Spearman correlation findings, suggesting that environmental factors like temperature and rainfall influence the nutritional composition of faba beans, with some accession-specific effects. The proximity of tannins, magnesium, and total polyphenol content to the rainfall arrow—given that the first CCA axis accounts for 65.1% of

the variance—indicates a potential positive effect of rainfall on their concentrations. On the other hand, temperature appears to be more closely associated with zinc and calcium, while pointing in the opposite direction from tannins, total polyphenol content, and magnesium, reinforcing the idea that higher temperatures may negatively affect these nutrients.



**Figure 4.** CCA Biplot illustrating the influence of temperature and rainfall on nutrient profiles across varieties and locations. Samples are reported in black, having specific symbols for each variety (reported in legend). The samples are grouped in ellipses representing location 1 (blue) and location 2 (yellow). Environmental variables as Temperature, Rainfall as well as Ph and yield per ha(kg) are represented as arrows in the biplot figure. Lastly, plant nutritional characteristics are reported in red.

The spatial distribution of faba bean varieties along the temperature and rainfall gradients suggests accession-specific responses to environmental factors. For instance, Quijote and Omeya aligned more closely with higher temperatures, suggesting that these accessions may sustain or even enhance nutrient accumulation under warmer conditions. In contrast, Navio6 and Prothabon were positioned closer to the rainfall vector, suggesting an association with cooler and wetter conditions. These trends highlight potential differences in environmental adaptation, though they represent relative positioning in ordination space rather than direct causal effects.

To further evaluate the role of environmental variables on the nutritional composition of faba bean varieties, a PERMANOVA was conducted on the CCA results (Table 3; Figure 4). The analysis indicates that grain yield significantly contributed to variation in mineral composition ( $F = 6.96, p = 0.001$ ), influencing the distribution observed in the CCA plot. Examination of vector directions confirmed strong correlations between temperature, rainfall, and specific nutritional components. The PERMANOVA results identified temperature ( $F = 7.48, p = 0.001$ ) and rainfall ( $F = 14.33, p = 0.001$ ) as highly significant drivers of variations in the nutritional composition of faba bean accessions.

**Table 3.** Permutational multivariate analysis of variance.

|                   | Df | ChiSquare | F       | Pr (>F)   |
|-------------------|----|-----------|---------|-----------|
| Yield (kg per ha) | 1  | 0.0017056 | 6.9571  | 0.001 *** |
| Temperature       | 1  | 0.0013148 | 7.4845  | 0.001 *** |
| Rainfall          | 1  | 0.0025170 | 14.3283 | 0.001 *** |
| Location          | 1  | 0.0004347 | 2.4743  | 0.016 *   |
| Residual          | 71 | 0.0124724 |         |           |

\* Significance codes: (\*\*\* for 0.001) (\* for 0.05).

## 4. Discussion

Our results suggest that environmental conditions are associated with differences in the nutritional composition of faba bean accessions. However, correlation does not imply causation, and other factors such as soil characteristics, plant phenotype, pest incidence, and agricultural practices may also influence these patterns [25–28]. The observed variations in nutrient accumulation across accessions coincided with specific temperature and rainfall conditions, which may have implications for current and future harvests under increasingly variable climatic conditions. Research indicates that the Earth’s average temperature has already increased by 1.5 °C, with 2024 recorded as the warmest year on record and the ten hottest years all occurring in the last decade [29]. In Andalusia, rising temperatures are evident: records from early 2025 (January–April) show that Location 1 experienced an average temperature of 18.3 °C, compared with the average temperatures of 14.9 °C measured during the same period in 2017–2019 [30].

In the CCA plot, the grain yield vector was positioned near Arrechana, Joya, and Quijote, suggesting that their mineral composition co-varies with grain yield. Accessions influenced by higher temperatures, such as Quijote and Omeya, tended to show elevated zinc and calcium levels but lower tannins, total polyphenol content, and magnesium content. Conversely, Navio6 and Prothabon—associated with higher rainfall—exhibited higher tannins, total polyphenols, and magnesium, but comparatively lower zinc and calcium. These trends reflect co-variation along environmental gradients rather than direct causal effects, as genotype-specific traits may also play a role. The CCA and PERMANOVA analyses provide evidence that environmental conditions strongly impact the nutritional composition of faba bean. These results suggest that certain varieties may be better adapted to climatic variation than others and offer a framework for identifying climate-resilient accessions for future cultivations. Confirming causal relationships would require multi-year field trials or controlled experiments.

The reduction in polyphenol concentrations was more apparent in warmer locations, consistent with previous studies showing that prolonged exposure to high temperatures can decrease polyphenol content due to their susceptibility to oxidation [31]. Heat stress induces the formation of reactive oxygen species (ROS), and polyphenols may be consumed in ROS scavenging to protect plant tissue [32,33]. While this mechanism could explain our observations, our study did not directly measure ROS activity.

Certain faba bean varieties accumulated higher tannins, zinc, and calcium. While extreme heat stress (42 °C) negatively impacts plant growth, moderate temperature increases can enhance photosynthesis and nutrient uptake [34]. Differences in mineral content could also stem from genotype-specific traits or interactions with plant growth-promoting bacteria (PGPB), which facilitate nutrient uptake [35]. PGPB contribute to phosphate mobilization and siderophore production, supplying plants with nitrogen, iron, phosphorus, and zinc—all of which play critical roles in plant tolerance to biotic and abiotic stress [36]. Under iron deficiency, plants activate alternative nutrient uptake strategies: Strategy I (rhizosphere acidification, which leads to iron reduction  $\text{Fe}^{2+}$ ) and Strategy II (release of phyto siderophores for iron chelation) [37,38]. These responses may also enhance zinc absorption [39]. However, our study did not assess microbial activity or physiological traits, limiting the interpretation of these mechanisms.

Nutrient accumulation patterns differed across sites. In Location 1, high temperatures could have caused mild heat stress on faba beans, resulting in elevated tannin levels. Faba bean is a cool-climate crop [40], and temperatures above 25 °C can reduce respiration efficiency, damage membranes, reduce biomass, and impair protein uptake [41]. Interestingly, Quijote and Omeya accumulated more zinc and calcium in Location 1, which is consistent with the activation of  $\text{Ca}^{2+}$  channels in legumes as a heat-shock response [40]. In contrast,

Navio6 and Prothabon in Location 2 accumulated more total polyphenols and magnesium, coinciding with higher rainfall. These observations reflect the combined effect of genotype and environmental factors [42].

It is known that the organic content of soil indirectly affects aeration and mechanical resistance of plant crops, which could impact the outcome of nutrient uptake in crops [43]. Vertisols, rich in minerals and clays, are highly productive, whereas Fluvisols have lower organic matter and are more drought-prone [42,44]. The differences observed in Location 1 may therefore be partly attributed to soil quality.

Our observations are consistent with studies on legumes across the Iberian Peninsula, where variety and variety  $\times$  environment interactions often exert stronger influence on nutrient uptake than single climatic factors [15,45]. This underscores the importance of considering both accession-specific responses and broader environmental context when interpreting nutritional variability in faba beans [46,47]. Another important factor in crop resilience is the intra- and interspecific variability within legumes. Although studies remain scarce [45], they provide valuable guidance for breeders and researchers to develop improved varieties that address climate-related challenges.

Overall, our results show that temperature and rainfall patterns influence both the nutritional composition and yield potential of faba bean accessions. Two-year observations suggest that Quijote and Omeya may perform better under higher temperatures, while Navio6 and Prothabon are more productive under wetter conditions but may be vulnerable in drier years. Extrapolating these trends to future scenarios suggests that climate shifts in Andalusian and other comparable Mediterranean regions may differentially impact faba bean yield and quality. A key strength of this study lies in underlining the importance of selecting accessions adapted to specific environments, which could serve as a first step towards the development of predictive models assessing crop performances under future climate scenarios.

The inclusion of CCA further strengthens the link between climate and nutrient uptake, reinforcing the role of temperature as a key driver of varietal differences. Evaluating these relationships is essential for selecting faba bean cultivars that can maintain nutritional quality under variable climates. Limitations of this study include the relatively small sample size and the exclusion of some varieties due to insufficient replicates, which may have influenced the observed patterns. Despite these constraints, our results provide a basis for further future research and may inform the development of breeding strategies for climate-resilient legumes.

Looking forward, high-protein crops such as legumes will play a crucial role as sustainable food sources. Expanding their use provides a promising alternative for diverse dietary needs, including those shaped by social or ethical considerations. Research of this kind supports advances in biotechnology and precision farming, contributing to the optimization of underutilized yet highly valuable crops.

**Supplementary Materials:** The following supporting information can be downloaded at <https://www.mdpi.com/article/10.3390/agriculture15181909/s1>: Table S1: Wilcoxon test for nutritional component levels in Location 1; Table S2: Wilcoxon test for nutritional component levels in Location 2.

**Author Contributions:** Conceptualization, J.O., E.P. and M.W.V.; study field design, E.B. and D.R.; field trials, E.B. and D.R.; methodology, E.B., D.R. and E.P.; formal analysis, J.O., G.F., E.P. and M.W.V.; data curation, G.F. and E.B.; writing—original draft preparation, J.O.; writing—review and editing, J.O., M.W.V., E.B. and D.R.; supervision, M.W.V., E.P. and D.R.; funding acquisition, M.W.V., E.P. and D.R. All authors have read and agreed to the published version of the manuscript.

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**Data Availability Statement:** The datasets presented in this article are not readily available because the data are part of an ongoing study. Requests to access the datasets can be directed to the corresponding author.

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**Conflicts of Interest:** The authors declare no conflicts of interest.

## Abbreviations

The following abbreviations are used in this manuscript:

|                |   |
|----------------|---|
| T              | Temperature   |
| R              | Rainfall  |
| K              | Potassium   |
| Ca             | Calcium   |
| Mg             | Magnesium   |
| Zn             | Zinc  |
| P              | Phosphorus  |
| Fe             | Iron  |
| Mn             | Manganese   |
| B              | Boron   |
| TPC            | Total polyphenol content  |
| TA             | Tannins   |
| S              | Saponins  |
| CCA            | Canonical correspondence analysis   |
| PERMANOVA      | Permutational multivariate analysis of variance   |
| CARs           | Carotenoids   |
| PA             | Phenolic acids  |
| GHG            | Greenhouse emissions  |
| N              | Nitrogen  |
| BNF            | Biological nitrogen fixation  |
| Ha             | Hectare   |
| EC             | European Commission   |
| EU             | European Union  |
| M              | Million   |
| pH             | Potential of hydrogen   |
| C              | Celsius   |
| mm             | Millimeters   |
| CSIC           | Spanish National Research Council   |
| S1/S2          | Season 1/2  |
| L1/L2          | Location 1/2  |
| Avg. Tmax/Tmin | Average temperature maximum/minimum   |
| OEVV           | General Subdirectorate of Agricultural Means of Production and Spanish Plant Variety Office |
| PC             | Protein concentration   |
| ICP-OES        | Inductively coupled plasma optical emission spectrometry                                    |
| GY             | Grain yield   |
| CC             | Correlation coefficient   |

|        |                                 |
|--------|---------------------------------|
| Df     | Degrees of freedom              |
| F      | F-statistic                     |
| Pr(>F) | P-value                         |
| ROS    | Reactive oxygen species         |
| PGPB   | Plant growth-promoting bacteria |

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