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Maize and Wheat Responses to the Legacies of Different Cover Crops under Warm Conditions

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Abstract: Cover crops (CC) have great potential to enhance the sustainability of agroecosystems. However, the wide range of possible rotations of CC and cash crops (CaC) means that important knowledge gaps persist on how CC affects CaC. We investigated the legacy effects of five common CC (three monocultures: vetch, melilotus, and barley, and two mixtures: barley-vetch and barley-melilotus) on two of the most important CaC, maize and wheat. A microcosm, semi-controlled experiment was established simulating warm, low-income Mediterranean conditions. After two cycles, soil physicochemical and microbial properties, as well as plant growth and nutrition variables, were measured at the CC early growth CaC stage. In maize, barley CC had the best soil microbial and nutritional legacy effects, which resulted in the highest biomass and nutrient status. In contrast, barley produced the worst results on wheat, showing the disadvantages of growing two crops from the same tribe consecutively. CC mixtures also did not offer a productive advantage over pure CC. Additionally, our findings suggest that archaea seem to play a role in increasing N and Zn content in maize shoots. Furthermore, shoot B contents showed highly significant regressions with the CaC biomass. These results can help select the appropriate CC in each case.

Keywords: maize; archaea; mineralization; nutrient availability; zinc; sulfur; boron

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1. Introduction

Cover crops (CC) provide numerous ecosystem services that improve the sustainability of agroecosystems and their adaptability to climate change [1,2]. The use of CC contributes to reducing soil erosion and runoff [3] and also to promoting soil organic C (SOC) content in soils, even to a greater extent than no tillage [4]. Hence, CCs are a key tool to support the Green Deal promoted by the European Union [5]. However, conventional tillage can decrease the beneficial impacts of CC [6], so combining CC and tillage reduction is recommended for soil C sequestration and climate change mitigation [7]. The CC type also influences soil C sequestration, with grass CC being more recognized for doing so than legume CC due to their higher biomass and C:N ratio [8]. However, the mass of SOC produced per kg of legumes can be slightly higher than that produced per kg of non-legumes [9]. Grass CC can also have a greater N recovery capacity than legume CC [10], which is important to scavenge the residual N and other nutrients during the time between one cash crop (CaC) and another [11]. However, the relatively high C:N ratio of grass CC means that the residue mineralization after termination may be slow and out of step with the needs of subsequent CaC, affecting nutrition and yield [10]. Therefore, the type of CC

can greatly modify the expected CC benefits, depending also on the particular soil and climatic conditions.

On the other hand, CC has a major effect on soil microbiology and a positive effect on microbial biomass [12]. Cover crops mainly influence soil microbial communities through (i) specific root exudates that can attract or repel microorganisms [13]; (ii) different quality and quantity of CC residues that determine the composition of the saprophyte communities [14]; and (iii) influencing soil moisture and temperature [15]. Interaction with subsequent CaC can greatly modify the microbial legacy effects of CC [16]. Legumes are of particular interest because of their ability to fix atmospheric N through their symbiosis with rhizobia and thus their potential to reduce synthetic N fertilization requirements [17]. On the other hand, certain non-legumes, such as barley, stand out in semi-arid Mediterranean environments for promoting arbuscular mycorrhizal fungi (AMF) and subsequent CaC nutrition [9]. Elucidating the factors that modulate microbial communities and encourage organisms that promote soil health, plant growth, and nutrition will help develop smarter agriculture and preserve natural resources.

A number of studies have proposed the use of CC mixtures, as crop diversification can not only improve ecosystem services but also increase the resilience of agroecosystems to climate change [18] and soil biodiversity [19], thus helping to achieve the aims of the EU's Biodiversity Strategy for 2030. Furthermore. The use of functionally diverse mixtures of CC, such as mixtures of legumes and grasses, is desirable to minimize the limitations associated with certain monocultures [20]. In this sense, mixtures of legumes with non-legumes are often selected as they reduce nitrate leaching while maintaining biological N_2 fixation capacity and high N availability in the soil [10]. In addition, legume mixtures with non-legumes often improve weed suppression relative to legume monocultures [21].

From an agronomic point of view, numerous studies have tried to determine how CC affects the subsequent CaC yield. The meta-analysis by Garba et al. [22] pointed out the great variability of CC effects, but on average, CC decreased soil water content by 18% and mineral N by 25%, which in dry environments decreased CaC yield by 12% on average. However, Abdalla et al. [13] indicated that CC mixtures could avoid yield reduction and even increase it by 13%. However, it is not yet clear which factors can drive the interactions between CC and CaC, as well as maize and wheat, in each soil-climate towards yield improvement and thus make cover cropping more economically sustainable.

Important knowledge gaps on how CC legacies interact with subsequent CaC in different environments prevent optimizing the CC's potential to improve agroecosystems [23]. Furthermore, current global warming prompts us to focus on agroecosystems with relatively high temperatures. Therefore, the main purpose of this work was to study the interaction of the two most produced CaC in the world (with more than 400 million hectares under cultivation): maize (C4 plant) and wheat (C3 plant) [24] with five common preceding CC, including two CC mixtures of a legume and barley under a warm low-income Mediterranean agroecosystem, where CC play a relevant role in increasing resilience to climate change. The starting hypotheses were: (i) the interaction effects between the legacy of five CC (plus a control without CC) with maize and wheat will be significantly different at the microbial level; (ii) the different adaptability to high temperatures of maize and wheat will result in markedly different CC legacies, so that the best CC for maize need not be the best CC for wheat; and (iii) CC mixtures will provide better results at the soil microbial and CaC levels, compared to monoculture CC.

2. Materials and Methods

2.1. Experimental Design

We studied the rotation of one CaC (maize or wheat) after different CCs. For this purpose, a randomized complete block design experiment with five replications or blocks was carried out in greenhouse conditions. The first factor studied five different CC: two legumes: Vetch (VET; *Vicia sativa* L.) and Melilotus (MEL; *Melilotus officinalis* L.); one grass, Barley (BAR; *Hordeum vulgare* L.); and two mixtures of grass and legume: barley plus vetch

(B+V) and barley plus melilotus (B+M). The control group without CC (CON) was also studied. The second factor was studied separately for two CaC, wheat (*Triticum aestivum* L., variety Nogal) or maize (*Zea mays*, variety Pioneer P1574), which were sown after the CC. In total, there were 12 treatments (6 CC × 2 CaC), which were randomly distributed in each block. This design allowed the block factor to absorb part of the spatial gradient of the greenhouse [25].

2.2. Soil and Growing Conditions

The soil used came from the top 20 cm of a Typic Calcixerept [26] (40°30′47″ N and 3°18′35″ W) under Bsk climate (Köppen-Geiger), with a markedly alkaline pH (8.35 ± 0.11 in 1:2.5 *w/v* aqueous suspension), low organic matter content (1.30% ± 0.03), and a loamy textural class (USDA classification). The soil was sieved at 1 cm and subsequently mixed with autoclaved river sand at a 2:1 *v/v* ratio to avoid problems of poor drainage after disturbance of the natural soil structure. The size of each microcosm was 18 × 18 × 25.5 cm. Direct seeding was used, and minimal inputs were provided during the experiment (Table 1). The sowing density in all CC was 312 plants m^{-2}. In the case of the mixed CC, 50% of the plants were barley, and the other 50% were legumes. Table 1 shows the chronogram of the activities carried out on the crops throughout the experiment, which was developed in a semi-controlled greenhouse whose luminosity, temperature, and volumetric humidity were recorded every five minutes. Prior to the present experiment, another cycle of CC and CaC was carried out on the same microcosms with the same treatments at lower temperatures. The results of which were published in Ulcuango et al. [16], and more information on the experiment can be found in this publication.

Table 1. Crop management schedule for the experiment in a semi-controlled greenhouse.

	March	April	May	June	July
Covered Crops sowing (15 March) and development for 11 weeks. *Mean aerial temperature during the CC: 18.5 °C*					
Sampling of cover crops and their termination (30 May)					
Wheat sowing (3 June) and development for 8 weeks					
Mean aerial temperature between CC termination and main sampling: 22.5 °C					
Maize sowing (24 June) and development for 5 weeks					
Fertilization with NH_4NO_3 91/0/0 (11 July)					
Irrigation: 112.5 ml per pot, 3 times per week (≈ 40 mm·month^{-1} of rain)					
Main Sampling and termination of the main crops (29 July)					

The CC residues were chopped and disposed of on the soil surface. Subsequently, direct seeding of the CaC was carried out, and six wheat plants and one maize plant were left per microcosm. After which a fertilization of 91/0/0 kg ha^{-1} with NH_4NO_3 (Table 1) was applied to maintain NPK levels above levels classified as very low according to rational fertilization criteria [27]. The greenhouse provided semi-controlled environmental conditions typical of a warm Mediterranean climate with reduced water availability. Thus, the average light intensity was 139.2 (µmol m^{-2} s^{-1}). The average temperature throughout the CC phase was 18.5 °C and 22.5 °C during the CaC phase. Irrigation carried out (Table 1) prevented the soil from reaching the permanent wilting point throughout the experiment or any visible leaching losses outside the microcosms.

2.3. Sampling and Analysis

Before CC termination, ground cover was quantified by the analysis of zenith photos of each microcosm using CobCal 2.0 software. After which the treatments were sampled. In addition, at the end of the experiment, main sampling was performed when maize was at phenological stage 3 and wheat was at phenological stage 2 [28] (Table 1).

For sampling, a 3.5 cm diameter cylindrical sampler with a side opening was used, which was stuck vertically into the ground, leaving each plant in the middle of the cylinder. This provided (i) the aerial part of the plants (shoot biomass), which was washed, dried

at 60 °C for 72 h, weighed, and milled for nutrient analysis, (ii) most of the roots, which were carefully separated, washed, weighed, and preserved at 4 °C for further analysis, and (iii) soil from 0 to 10 cm depth, which was denominated rhizospheric soil (soil between 0 and 17.5 mm away from the root surface). After homogenization, one part of the soil was preserved at −20 °C for microbial analysis; a second fraction was preserved at 4 °C for extraradicular hyphal length analysis; and a third fraction was air dried, sieved at 2 mm, and milled when necessary.

Measurements of pH and electrical conductivity at 25 °C (EC) were made in aqueous soil extracts, 1:2.5 *w/v*. The concentrations of total N in both soil and shoots were determined by the Kjeldahl method [29]. The rest of the macronutrients and micronutrients were extracted using the Mehlich-3 procedure [30]. Subsequently, both soil and shoot nutrients were analyzed by Inductively Coupled Plasma Optical Emission Spectrometry (iCAP 6500-duo 200 spectrometry, Thermo Elemental Co., Iris Intrepid II XDL, Waltham, MA, USA. The concentrations of soil and shoot macronutrients (Ca, K, Mg, N, P, and S), as well as the micronutrients in soil (Co, Fe, Mn, Na, Ni, and Zn), and in shoot (B, Cu, Fe, Mn, Na, and Zn), were obtained. The nutrient content extracted by the aerial part of the crops in each microcosm was obtained by multiplying the dry shoot biomass by the shoot concentration of each nutrient.

The procedure of Vierheilig et al. [31] was applied to stain AMF structures on crop roots, and subsequently, the method of extended intersections was used to quantify the mycorrhizal colonization [32]. Mycelium or extraradicular hyphal length in soil was determined following the adaptation of García-González et al. [33] based on the method of Jakobsen et al. [34]. Substrate-induced soil respiration (SIR) was determined by the method of Alef and Nannipieri [35] after incubating the samples for 4 h at 22 °C with a NaOH trap. In addition, dissolved organic carbon (DOC) was extracted from the soil with 0.5 M potassium sulphate and determined by wet oxidation with potassium dichromate [36].

In addition, at the end of the experiment prior to the main sampling, three measurements of the soil penetration resistance (top 5 mm) were made in each microcosm using a pocket penetrometer (ST 315, 6.35 mm diameter, Farnell, Lainate, Italy), together with soil temperature and humidity measurements in the top 5 cm. To obtain soil moisture, the ECH2O 5TM sensor (Decagon Devices, Inc., Washington, DC, USA) was used, which provided the volumetric water content by measuring the dielectric constant of the soil at a frequency of 70 MHz [37].

Finally, DNA was extracted from the soil samples of the main sampling (previously stored at −20 °C) using the PowerSoil® DNA isolation kit (Mo-Bio Laboratories, Carlsbad, CA, USA). The extracted DNA was used to estimate total bacteria, total fungi, total archaea, and the Glomeromycetes via qPCR. The reagent mix used to run the qPCR was 20 µL containing 10 µL of the KAPA SYBR® FAST qPCR Master Mix (2×) kit (Kapa Biosyistems, Washington, MA, USA), 4.2 µL of nuclease-free water, 0.4 µL of each primer (10 µM), and 5 µL of pre-diluted template DNA using a real-time system (LightCycler® 480-Roche). The qPCR standards for each molecular target were obtained using a serial (10-fold) dilution of plasmids carrying a single cloned target gene or a relevant part of it. The genes were cloned in P-GEM T-easy (Promega, Madison, WI, USA). In this study, the molecular markers used were the 16S rRNA genes for bacteria and archaea, the ITS region gene for total fungi, and to estimate the Glomeromycetes class (also known as Glomeromycota), the small subunit (SSU) rRNA gene was used [38–41]. The primers used for each marker are shown in Table S1. The standard curves generated in each reaction were linear (serial dilutions of plasmids from 102 to 107 gene copies) with $r^2 > 0.98$. The amplification efficiencies of all reactions for gene quantification were in the range of 80 to 100%. Copy numbers of total bacteria, archaea and fungi and Glomeromycetes were expressed as Log_{10} gene copy numbers per gram of dry soil (Log copies g^{-1}).

2.4. Statistical Analysis

Variables were tested for normality and homoscedasticity (with Levene's test) with 95% confidence, applying the Box-Cox transformation when necessary (i.e., EC, DOC, soil P, S, and Zn; plant Fe and Na in maize; plus, soil Fe, K, and S; plant Mg and Glomeromycetes in wheat). To analyze the effect of the study factors on the variables as well as the interaction between these factors, a generalized linear model for a randomized block design was used. To reject the null hypothesis of equality of means, the ANOVA technique was used, followed by Fisher's least significant difference test (LSD) to compare the means of the different levels within a factor. The analyses were carried out by separating maize from wheat due to the strong interaction between CC and CaC found in most of the variables. In addition, linear regressions with five independent variables at maximum were calculated, and the equation with the highest adjusted r^2 within each subset of variables [(i) microbial, (ii) soil, and (iii) plant] was selected to relate the biomass production of the CaC to the variables. Generalized linear models, linear regressions, and Pearson correlations were calculated using Statgraphics Centurion XVIII software (Statgraphics Technologies, Inc., The Plains, VA, USA).

Principal component analyses (PCA) were performed to reduce the number of variables with which to describe the variability of the three subsets of variables. In this way, we were able to reduce and represent each data set to only two principal components without linear correlation to visualize the differences between treatments. The PCA analyses were performed with the free R software [42] using the facto extra package [43]. With this software, confidence ellipses around each treatment at the 95% confidence level were included in the representation of the first two components (biplot).

3. Results

Initially, the CC with the highest aerial biomass production was BAR, and the lowest was MEL, for both maize and wheat rotations at CC termination. (Table S2a,b). Later, most variables studied at final sampling showed significant interactions between the two study factors (type of CC vs. type of CaC), indicating a different response of wheat (C3 plant) and maize (C4 plant) to the CC legacies at the time of final sampling. Therefore, the results of maize and wheat were studied and presented separately.

3.1. Microbial Variables in Maize after Cover Crops

In the final sampling, all CC treatments showed higher AMF colonization than CON (without CC) in maize and wheat roots (Table 2a,b). In maize, BAR and B+V were the treatments with the highest AMF colonization. However, these same treatments had the lowest bacterial abundance in the soil. Meanwhile, the legumes VET and MEL, together with CON, provided the highest contents of bacteria, fungi, and Glomeromycetes in maize soil (Table 2a).

The biomass of the CC (Table S2) had a significant influence on the subsequent maize and its microbial variables. Thus, CC biomass showed positive correlations with aerial and root biomass in maize ($r = 0.44$ *; $r = 0.49$ **, respectively), as well as with AMF colonization ($r = 0.44$ *) and soil archaeal abundance ($r = 0.61$ ***) in maize. In addition, aerial biomass of CC was negatively correlated with bacterial ($r = -0.44$ *) and Glomeromycetes ($r = -0.65$ ***) abundances found in the maize soil (Table 2a).

The first two principal components of the maize microbial variables explained 58% of their variability (Figure 1a). Here, CON, with a relatively high bacterial abundance, clearly differed from the rest of the treatments. In Figure 1a, BAR was the furthest away from the CON as it was located in the opposite quadrant, which was characterized by a high archaeal abundance. Differences were also observed between the two CC mixtures (B+V and B+M), although they were found to be very close in the biplot. However, there were no differences between the two legume monoculture CC treatments (MEL and VET), as their corresponding confidence ellipses overlapped (Figure 1a).

Table 2. Microbial properties under (a) maize and under (b) wheat.

Previous CC	AMF Colonization (%)			Mycelium Length (cm g^{-1})			Bacteria (Log Copies 16S g^{-1})			Fungi (Log Copies ITS g^{-1})			F:B (Log (ITS:16S))			Glomeromycetes (Log Copies g^{-1})			Archaea (Log Copies g^{-1})			SIR * (mg C-CO_2 $kg^{-1}h^{-1}$)		
(a) Under maize																								
CON	13	±2.4	a	5.93	±2.54	a	9.033	±0.018	c	6.705	±0.038	c	−2.33	±0.03	ab	5.67	±0.03	f	6.59	±0.03	a	2.21	±1.37	a
VET	22	±5.0	bc	6.01	±2.41	a	9.038	±0.032	c	6.946	±0.054	e	−2.09	±0.08	c	5.43	±0.04	e	7.05	±0.02	c	2.12	±0.96	a
MEL	20	±5.2	b	6.59	±1.46	a	8.942	±0.053	b	6.938	±0.035	e	−2.00	±0.06	cd	5.34	±0.04	d	6.67	±0.04	a	1.93	±1.08	a
BAR	26	±4.5	c	7.51	±2.02	a	8.791	±0.128	a	6.836	±0.028	d	−1.95	±0.14	d	4.99	±0.04	b	7.10	±0.04	c	2.02	±1.03	a
B+V	34	±6.7	d	6.97	±2.29	a	8.77	±0.097	a	6.531	±0.039	b	−2.24	±0.09	b	5.07	±0.03	c	6.88	±0.03	b	1.86	±0.86	a
B+M	22	±6.3	bc	6.56	±2.25	a	8.801	±0.051	a	6.38	±0.055	a	−2.42	±0.10	a	4.39	±0.04	a	6.91	±0.13	b	1.97	±0.59	a
(b) Under wheat																								
CON	8.8	±4.3	a	4.33	±1.97	a	8.424	±0.025	a	6.302	±0.178	a	−2.201	±0.030	a	4.407	±0.041	a	7.1	±0.052	a	2.14	±1.22	a
VET	14.6	±3.6	bc	5.91	±1.26	ab	8.852	±0.025	d	7.337	±0.027	f	−1.515	±0.033	e	4.524	±0.035	b	7.39	±0.041	c	1.73	±1.18	a
MEL	16.8	±2.2	bc	6.41	±1.05	ab	8.664	±0.017	C	6.838	±0.030	b	−1.826	±0.047	b	5.789	±0.047	d	7.24	±0.038	b	1.78	±0.97	a
BAR	13.8	±3.9	ab	7.23	±1.60	bc	8.619	±0.027	B	6.952	±0.044	c	−1.667	±0.060	d	6.003	±0.041	e	7.37	±0.030	c	1.95	±1.12	a
B+V	19.4	±4.4	c	6.31	±1.93	ab	8.822	±0.040	D	7.071	±0.019	d	−1.751	±0.053	c	6.032	±0.032	e	7.36	±0.043	c	2.33	±1.19	a
B+M	19.6	±5.0	c	8.87	±2.45	c	8.933	±0.014	E	7.250	±0.017	e	−1.684	±0.028	d	5.599	±0.036	c	7.06	±0.020	a	2.04	±0.89	a

±; standard deviation of each mean (without taking into account the blocking factor). Different letters after the means indicate significant differences with $p < 0.05$ according to LSD; CON: control without CC; VET: vetch; MEL: melilotus; BAR: barley; B+V: barley with vetch; and B+M: barley with melilotus. * Substrate-induced respiration.

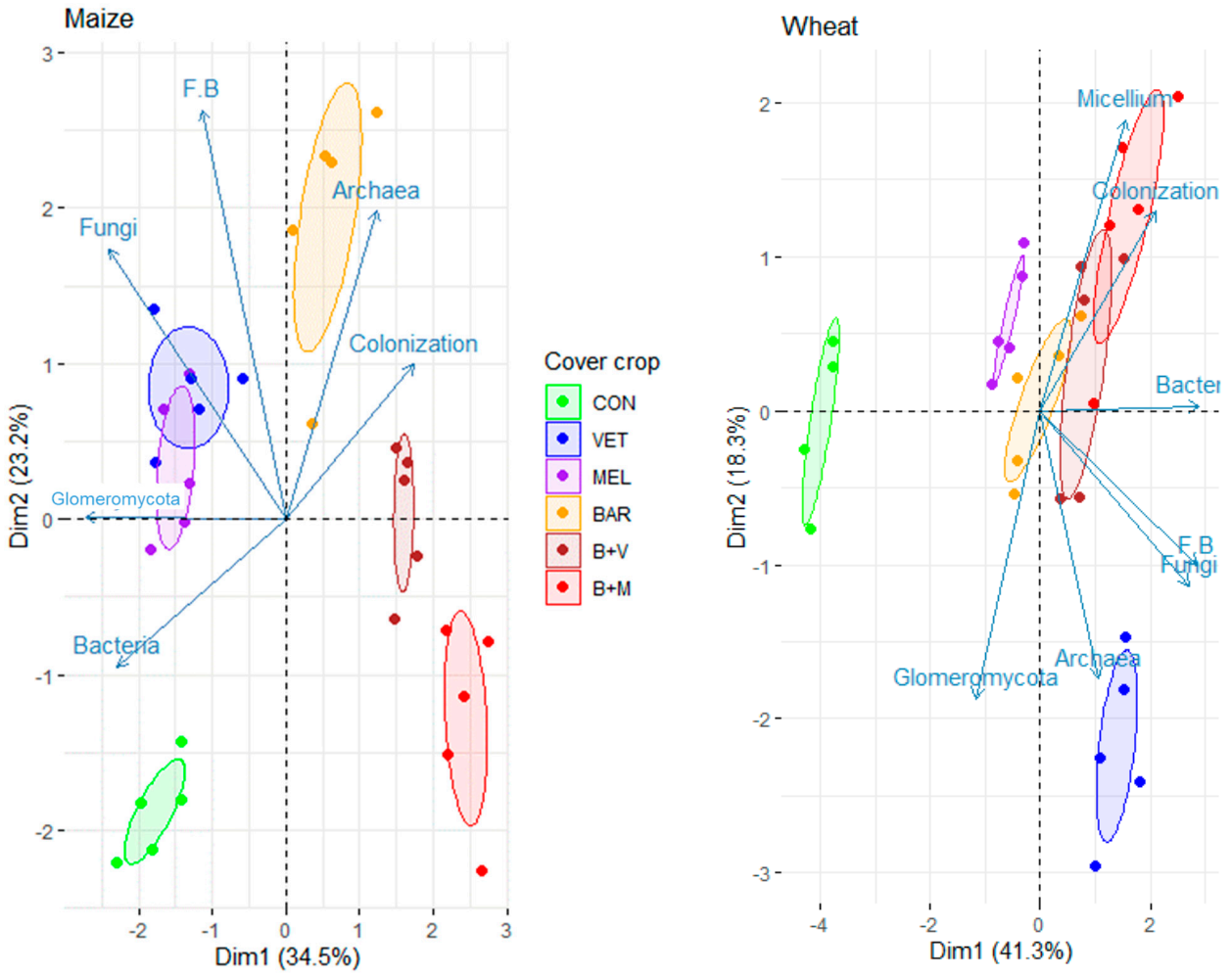


Figure 1. Principal component analysis biplot of microbial variables and confidence ellipses of each treatment (CON: control without cover crop; VET: vetch; MEL: melilotus; BAR: barley; B+V: barley with vetch; and B+M: barley with melilotus). In (**a**) maize and in (**b**) wheat at the time of final sampling. (F.B; fungi to bacteria ratio).

Despite the importance of the microbial variables, no significant linear regression was found relating maize aerial biomass to the microbial variables studied.

3.2. Microbial Variables in Wheat after Cover Crops

The treatments of mixtures (B+V and B+M) showed the highest AMF colonization of wheat roots eight weeks after seeding (Table 2b). However, except for colonization and SIR, they showed contrasting performances. Thus, B+M showed the highest mycelium length and archaeal abundance, while B+V, in these two variables, showed very low values close to those of CON. On the other hand, VET showed the highest fungal abundance, archaeal abundance, and F:B ratio. In wheat, as in maize, CC biomass had positive correlations with AMF colonization (r = 0.48 **), fungal (0.53 **), and archaeal (0.50 **) abundances. However, only in wheat rotation, CC biomass production (Table S2) showed positive correlations with the abundances of bacteria and Glomeromycetes (Table 2b) (r = 0.55 ** and 0.41 *, respectively).

In wheat, the PCA results explained 60% of the variability of microbial variables. As in maize, CON was separated from the other treatments (Figure 1b). The treatment closest to CON was MEL. While VET, with its greater abundance of fungi and archaea, was the treatment furthest away from CON. In this case, the B+V and B+M treatments did not differ from each other. In addition, B+V showed no difference with BAR.

3.3. Effects of Soil Properties on Crop Biomass

The CC also had effects on fundamental soil properties that lasted until the final sampling. Thus, in the rotation with maize and five weeks after seeding, CC biomass production was positively correlated with soil moisture (r = 0.37 *). The wettest soil was BAR (Table 3a). On the other hand, penetration resistance was negatively correlated with CC biomass and maize biomass (r = −0.48 **, r = −0.58 ***, respectively).

Table 3. Soil properties under (a) maize and under (b) wheat.

Previous CC	Soil Moisture (%v)			Soil Temperature (°C)			pH			EC (µS cm^{-1})			DOC (mg kg^{-1})			Penetration Resistance (kg cm^{-2})		
(a) Under maize																		
CON	9.26	±1.67	bc	25.24	±0.73	a	7.68	±0.51	a	493	±263	a	30.5	±2.0	a	2.15	±0.19	ab
VET	8.3	±0.42	ab	25.25	±0.40	a	7.88	±0.42	ab	345	±183	a	30.3	±8.4	a	2.34	±0.78	b
MEL	7.41	±0.83	a	25.71	±0.82	a	8.29	±0.33	c	381	±83	a	32.3	±2.7	a	2.25	±0.87	ab
BAR	10.09	±1.01	c	25.22	±0.79	a	8.15	±0.11	bc	348	±143	a	34.6	±9.9	a	1.51	±0.82	ab
B+V	7.62	±0.53	a	25.47	±0.46	a	7.92	±0.12	abc	433	±121	a	31.2	±1.7	a	2.15	±0.60	ab
B+M	9.32	±1.60	bc	25.56	±0.53	a	7.93	±0.50	abc	341	±164	a	28.4	±4.0	a	1.46	±0.85	a
(b) Under wheat																		
CON	7.76	±0.72	b	25.24	±0.79	ab	8.1	±0.25	a	386	±167	a	30.6	±6.7	a	3.83	±0.45	ab
VET	7.52	±0.51	b	25.29	±0.78	ab	8.02	±0.27	a	457	±255	a	39.1	±10.3	a	4.9	±0.94	b
MEL	7.21	±0.79	ab	25.45	±0.64	b	8.09	±0.12	a	437	±153	a	33	±6.8	a	3.65	±0.79	ab
BAR	8.08	±0.83	b	24.82	±0.61	a	8.08	±0.17	a	348	±140	a	34.5	±11.9	a	3.87	±1.25	ab
B+V	7.49	±0.51	b	25.76	±0.50	b	8.03	±0.21	a	396	±140	a	53.2	±10.0	b	3.8	±1.22	ab
B+M	6.52	±0.45	a	25.23	±1.10	ab	8.44	±0.22	b	268	±152	a	32.1	±5.1	a	3.53	±0.73	a

±; standard deviation of each mean (without taking into account the blocking factor). Different letters after the means indicate significant differences with $p < 0.05$ according to LSD; CON: control without CC; VET: vetch; MEL: melilotus; BAR: barley; B+V: barley with vetch; and B+M: barley with melilotus. EC: Electrical conductivity. DOC: dissolved organic carbon.

The CC treatments, compared to the control, produced changes in the soil K, Mg, N, P, and S in maize (Table 4a). Thus, the highest soil N was observed in the B+V treatment and the lowest in CON. On the contrary, the highest soil S concentration was measured in CON and the lowest in B+V and B+M. Cover crops, compared to the control, also induced modifications in three micronutrients (Co, Na, and Zn). Of them, Co stood out for its correlation with the soil concentration of three other nutrients (Ca, N, and P). Additionally, soil Co and P s were inversely proportional to CC biomass production (r = −0.49 ** and −0.66 ***, respectively). On the other hand, a highly significant linear regression (***) was obtained relating some of the soil variables to maize shoot biomass production (Equation (1)).

$$\text{Maize Biomass (kg ha}^{-1}) = 2192 - 158.7 \times \text{Penetration Resistance} + 9.298 \times \text{Fe} - 1120 \times \text{S}^{-0.138} + 0.2551 \times \text{N} - 98.51 \times \text{pH} \ (p = 0.000, r^2 = 0.62) \quad (1)$$

(The units of the independent variables are those indicated in Tables 3 and 4).

The PCA of the soil properties in maize explained 47% of the variability in the data and revealed no differences between the six CC treatments.

In the case of wheat, B+M showed the lowest volumetric soil moisture, the highest pH, and the lowest penetration resistance (Table 3b). In addition, DOC was positively correlated with the biomass production of the previous CC (r = 0.45 *). In relation to the soil nutrients in wheat, the VET treatment showed the lowest concentrations of Ca, Mg, Mn, Na, and Ni (Table 4b). In contrast, BAR showed the highest concentrations of soil Ca, Mg, Co, and Na, while B+M showed the highest concentrations of S, Co, and Zn.

The PCA of soil properties in wheat explained 43% of the data variability, and the biplot only showed that CON, with its higher S concentration, was different from B+M. Finally, as in maize, the aerial CC biomass production showed correlations with some soil nutrients in wheat, e.g., with S (r = 0.44 *) and Zn (r = 0.44 *).

Table 4. Concentrations of the macro and micro nutrients extracted with Mehlich-3 in the (a) maize soil and (b) the wheat soil.

(a) Under maize																				
Previous CC	**Ca**			**K**			**Mg**			**N***			**P**			**S**				
	(mg kg^{-1})																			
CON	887	±72	a	100.5	±5.6	a	159.7	±11.4	b	381	±199	a	32.9	±2.4	b	19.4	±10.3	c		
VET	834	±61	a	103	±3.1	a	155.1	±7.6	ab	525	±158	abc	33.1	±4.2	b	12.9	±3.0	abc		
MEL	862	±85	a	99.3	±1.8	a	145.8	±6.6	a	611	±294	abc	30.9	±1.5	b	10.8	±3.1	ab		
BAR	894	±127	a	111.9	±7.7	b	155.3	±13.7	ab	693	±207	bc	27.0	±1.3	a	15.7	±4.2	bc		
B+V	847	±88	a	103.4	±6.3	a	159.8	±10.5	b	715	±99	c	31.5	±1.7	b	9.6	±4.2	a		
B+M	868	±67	a	95.8	±8.4	a	148.9	±11.5	ab	418	±191	ab	27.6	±1.9	a	9.1	±2.8	a		
Previous CC	**Co**			**Fe**			**Mn**			**Na**			**Ni**			**Zn**				
	(mg kg^{-1})																			
CON	0.889	±0.041	c	58.5	±9.3	a	51.3	±4.6	a	58.6	±15.2	b	0.626	±0.058	a	2.51	±0.85	ab		
VET	0.841	±0.059	abc	63.5	±9.9	a	50.1	±2.8	a	45.5	±14.0	ab	0.625	±0.035	a	2.86	±0.35	b		
MEL	0.816	±0.045	ab	60.4	±7.1	a	48.1	±2.4	a	51.9	±4.9	ab	0.607	±0.024	a	2.89	±0.70	b		
BAR	0.807	±0.056	ab	66.5	±9.4	a	50.3	±5.6	a	54.5	±13.4	ab	0.614	±0.048	a	2.19	±0.23	a		
B+V	0.861	±0.039	bc	65.0	±5.5	a	50.7	±2.0	a	50.3	±21.5	ab	0.625	±0.031	a	2.5	±0.42	ab		
B+M	0.800	±0.026	a	62.3	±7.7	a	47.5	±1.5	a	40.8	±9.6	a	0.589	±0.032	a	2.46	±0.22	ab		
(b) Under wheat																				
Previous CC	**Ca**			**K**			**Mg**			**N***			**P**			**S**				
	(mg kg^{-1})																			
CON	840	±55	ab	96.8	±9.7	a	148.7	±10.3	a	416	±329	a	31.9	±3.4	ab	11.8	±5.3	a		
VET	792	±97	a	95.5	±9.0	a	141.6	±18.3	a	552	±217	a	33.0	±3.3	b	14.1	±7.6	a		
MEL	838	±62	ab	97.3	±20.5	a	146.9	±14.6	a	559	±103	a	29.6	±2.2	a	16.5	±10.2	ab		
BAR	947	±91	c	97.4	±10.1	a	163.7	±8.2	c	624	±239	a	30.5	±2.8	ab	21.3	±3.6	b		
B+V	844	±85	ab	94.6	±3.8	a	151.5	±13.4	ab	573	±171	a	29.8	±1.8	ab	16.5	±5.0	ab		
B+M	904	±47	bc	104.5	±10.2	a	160.1	±6.2	bc	586	±249	a	30.7	±2.1	ab	24.9	±13.0	b		
Previous	**Co**			**Fe**			**Mn**			**Na**			**Ni**			**Zn**				
CC	**(mg kg^{-1})**																			
CON	0.818	±0.058	ab	57.7	±6.9	a	47.6	±3.5	ab	44.2	±16.6	ab	0.58	±0.032	ab	2.24	±0.53	a		
VET	0.774	±0.089	a	57.3	±6.3	a	45.7	±5.2	a	37.3	±21.7	a	0.558	±0.044	a	2.95	±0.89	bc		
MEL	0.817	±0.080	ab	56.1	±13.7	a	48.4	±5.3	ab	42.1	±22.3	a	0.595	±0.066	abc	2.58	±0.66	ab		
BAR	0.864	±0.090	b	54.7	±8.8	a	50.7	±4.5	b	63.1	±13.0	b	0.610	±0.030	bc	2.65	±0.74	ab		
B+V	0.800	±0.079	ab	56.2	±4.1	a	47.6	±4.2	ab	55.5	±7.6	ab	0.584	±0.035	ab	2.54	±0.48	ab		
B+M	0.870	±0.054	b	62.7	±9.7	a	51.2	±3.2	b	52.8	±9.0	ab	0.633	±0.038	c	3.23	±0.72	c		

±; standard deviation of each mean (without taking into account the blocking factor). Different letters after the means indicate significant differences with $p < 0.05$ according to LSD; CON: control without CC; VET: vetch; MEL: melilotus; BAR: barley; B+V: barley with vetch; and B+M: barley with melilotus. N*; total Kjeldahl nitrogen.

3.4. Maize Biomass and Shoot Nutrient Contents

The BAR treatment provided the highest maize aerial biomass production but was not significantly different from the control. BAR also had the highest fresh maize root biomass, this time 73% higher than that in CON (Table 5a). In contrast, the treatment with the worst maize biomass production was MEL. The MEL treatment showed no differences with CON in any of the plant parameters analyzed and showed the lowest shoot N, B, Ca, and Fe contents in maize. In contrast, BAR showed the highest contents of Ca, K, Mg, N, B, and Zn. While B+M stood out because its maize was able to extract the highest Na contents. Subsequently, a highly significant linear regression ($p < 0.001$) was obtained relating maize biomass production to the content of shoots N and B.

$$\text{Maize Biomass (kg ha}^{-1}) = -153.1 + 10.93 \times \text{N} + 5.969 \times \text{B} \ (p = 0.000, \ r^2 = 0.92) \quad (2)$$

Table 5. Aerial biomass, root biomass and macro and micro nutrient contents in (a) maize shoots and in (b) wheat shoots.

(a) Under maize

Previous CC	Dry aerial biomass (kg ha^{-1})	Ca	K	Mg	N*	P	S
		(mg microcosm^{-1})					
CON	950 ±75 ab	10.7 ±1.1 ab	57.1 ±14.0 ab	5.64 ±2.17 a	74.8 ±4.8 a	5.57 ±0.81 a	5.58 ±1.40 A
VET	1000 ±220 ab	10.5 ±1.7 a	45.7 ±14.6 a	6.71 ±3.03 ab	81.5 ±13.2 ab	5.86 ±1.06 a	5.76 ±1.64 a
MEL	869 ±206 a	9.7 ±2.3 a	46.6 ±17.8 a	6.2 ±3.05 ab	74.6 ±15.4 a	5.59 ±1.46 a	5.26 ±1.88 a
BAR	1141 ±149 b	13 ±1.7 b	61.7 ±20.4 b	7.27 ±1.99 b	91.7 ±8.8 b	6.84 ±1.84 a	5.9 ±1.27 a
B+V	1015 ±100 ab	10.4 ±2.6 a	46.6 ±13.2 a	6.19 ±2.47 ab	85.3 ±5.8 ab	6.22 ±1.22 a	5.53 ±1.77 a
B+M	1096 ±213 ab	11.4 ±1.6 ab	53.1 ±16.4 ab	7.12 ±2.72 ab	88.1 ±13.9 ab	6.8 ±1.45 a	6.68 ±2.03 a
Previous CC	**Root biomass (kg ha^{-1})**	**B**	**Cu**	**Fe**	**Mn**	**Na**	**Zn**
		(µg microcosm^{-1})					
CON	741 ±272 a	43.9 ±5.4 ab	18.4 ±1.5 a	278 ±107 a	232 ±35 a	315 ±166 a	76.3 ±7.8 a
VET	843 ±219 a	39.8 ±10.1 a	19.5 ±2.7 a	302 ±137 a	262 ±58 ab	629 ±497 abc	96.1 ±19.5 ab
MEL	831 ±103 a	39.6 ±10.6 a	18 ±5.0 a	294 ±150 a	234 ±71 a	349 ±282 a	87.3 ±21.6 ab
BAR	1281 ±323 b	51.8 ±6.4 b	20.7 ±2.7 a	426 ±247 bc	306 ±27 b	435 ±140 ab	111.5 ±16.9 b
B+V	898 ±229 ab	38.7 ±6.7 a	19 ±4.3 a	322 ±139 ab	250 ±54 ab	713 ±593 bc	102.7 ±15.4 b
B+M	1049 ±439 ab	48.6 ±7.8 ab	20.8 ±5.5 a	470 ±217 c	282 ±56 ab	817 ±463 c	110.1 ±17.7 b

(b) Under wheat

Previous CC	Dry aerial biomass (kg ha^{-1})	Ca	K	Mg	N*	P	S
		(mg microcosm^{-1})					
CON	1144 ±283 c	12.3 ±3.36 b	79.3 ±32.5 c	5.29 ±2.05 a	111.8 ±26.0 bc	6.38 ±1.49 bc	7.42 ±3.24 bc
VET	1125 ±104 bc	11.1 ±2.41 ab	62.1 ±15.5 b	5.93 ±2.88 a	107.6 ±22.8 bc	7.05 ±1.42 bc	6.87 ±2.20 bc
MEL	1078 ±266 bc	11.3 ±3.01 ab	62.9 ±25.3 b	6.01 ±2.75 a	113.3 ±28.4 c	7.44 ±2.05 c	7.52 ±2.97 c
BAR	718 ±157 a	8.1 ±1.86 a	35.1 ±13.5 a	4.39 ±2.00 a	66.1 ±11.9 a	4.59 ±0.49 a	4.44 ±1.44 a
B+V	848 ±163 a	9.3 ±2.2 ab	47.4 ±19.6 b	4.74 ±2.01 a	88.7 ±15.1 ab	5.71 ±1.44 ab	5.74 ±2.13 b
B+M	910 ±162 ab	10.1 ±1.84 ab	52.8 ±16.9 b	5.54 ±1.98 a	96.4 ±17.0 bc	6.79 ±1.61 bc	6.64 ±2.40 bc
Previous CC	**Root biomass (kg ha^{-1})**	**B**	**Cu**	**Fe**	**Mn**	**Na**	**Zn**
		(µg microcosm^{-1})					
CON	1236 ±230 ab	50.2 ±12.4 c	22.2 ±6.8 bc	466 ±292 bc	261 ±58 b	508 ±362 ab	88.5 ±24.3 ab
VET	1328 ±180 b	47.2 ±12.5 bc	22.3 ±5.2 bc	332 ±146 b	265 ±57 b	685 ±534 abc	123.2 ±30.9 c
MEL	1156 ±324 ab	45.6 ±12.2 abc	24.0 ±6.9 c	498 ±305 c	278 ±65 b	927 ±758 bcd	125.3 ±41.1 c
BAR	1066 ±131 ab	32 ±7.3 a	15.4 ±4.0 a	214 ±85 a	173 ±38 a	441 ±324 a	73.3 ±16.6 a
B+V	991 ±183 a	35.5 ±7.7 ab	18.1 ±5.4 ab	318 ±184 ab	210 ±43 ab	1058 ±805 cd	100.7 ±33.5 abc
B+M	1002 ±164 a	37.3 ±7.2 ab	21 ±5.1 bc	440 ±261 bc	240 ±38 ab	1222 ±.931 d	114.1 ±34.1 bc

±; standard deviation of each mean (without taking into account the blocking factor). Different letters after the means indicate significant differences with $p < 0.05$ according to LSD; CON: control without CC; VET: vetch; MEL: melilotus; BAR: barley; B+V: barley with vetch; and B+M: barley with melilotus. N*; content of total Kjeldahl nitrogen per microcosm.

(The units of the independent variables are those indicated in Table 5a).

A significant linear regression was also found that related the N content in maize to three microbial variables:

$$\text{N in maize (mg microcosm}^{-1}) = 206.2 - 30.18 \times \text{Bacteria} + 20.11 \times \text{Archaea} + 3.366 \times \text{SIR} \ (p = 0.018, r^2 = 0.32) \quad (3)$$

(The units of the independent variables are those indicated in Table 2a).

Among the elements studied in maize, Fe presented a positive correlation between its soil concentration and the shoot Fe content in maize (r = 0.41 *). Finally, the PCA of the maize plant variables explained 74% of the data variability, but the biplot only showed that CON was different from BAR (Figure S1a).

3.5. Wheat Biomass and Shoot Nutrient Contents

The VET and CON treatments showed the highest root weights and shoot biomass of wheat, while the lowest were found in BAR and B+V (Table 5b). Wheat from the BAR treatment, in contrast to maize, showed the lowest contents of shoot elements (Table 5b). In contrast, MEL showed the highest contents of N, P, S, Cu, Fe, Mn, and Zn. The CON

treatment also showed high contents in most of the elements analyzed and reached the maximum values in Ca, K, and B. While the B+M mixture stood out for extracting the highest Na content in wheat, as was also observed in maize. Shoot Na in wheat showed a positive correlation with CC biomass production (r = 0.46 *).

As with maize, a highly significant linear regression ($p < 0.001$) was found relating aerial biomass production of wheat to shoot N and B content (Equation (4)).

$$\text{Wheat Biomass (kg ha}^{-1}) = 8.941 + 5.776 \times \text{N} + 9.661 \times \text{B} \ (r^2 = 0.96, p = 0.000) \quad (4)$$

(The units of the independent variables are those indicated in Table 5b).

The PCA of wheat plant variables explained 86% of the variability in the data, but the biplot only showed that VET was different from BAR as the latter had very low macro- and micronutrient contents in shoots (Figure S1b).

4. Discussion

4.1. Crops Shape Soil Microbiomes

Under low-input, warm Mediterranean conditions, each type of CC had its own specific legacy effect on the soil microbiome, with greater differences for maize than for wheat. Firstly, CON without CC presented a lower AMF colonization in both CaC (Table 2), as AMF are obligate symbionts and were seriously impaired by the lack of a host during the CC period [16]. Moreover, different from CC treatments, the absence of plants in CON resulted in a lack of exudates, residues, and CO_2 emissions from roots, as well as a lack of nutrient scavenging. All of which caused the CON to clearly differ from CC treatments in the soil microbial variables for both maize and wheat rotations (Figure 1a,b) [12]. Meanwhile, the different CC types were able to shape the soil microbiome by providing specific organic compounds, including allelopathic and root exudate signaling compounds (directly or via other organisms), or by modifying the soil's abiotic environment [19,44]. For maize, BAR provided the greatest CC residue amount (Table S2) and induced the most changes in microbial variables compared to the control (Table 2a). For example, BAR provided the highest AMF colonization, which especially affects C4 grasses, such as maize, as they are usually adapted to warm environments with high light intensity, where the role of AMF is fundamental for nutrient acquisition, resistance to water stress, and antagonism of fungal pathogens [19].

Similar to CC, the CaC roots and their exudates also played a crucial role in microbial variables measured at the final sampling [45]. According to Walker et al. [46], numerous substances and between 5% and 21% of all photosynthetically fixed C are secreted by roots into the soil, which inevitably affects soil biochemical properties. These exudates play a fundamental role by enriching the rhizospheric soil with key elements for microbial and/or plant activity [46]. Thanks to these exudates, and contrary to what might be expected in an experiment where all the microcosms initially had the same soil, some nutrients showed positive correlations between the content extracted by the aerial biomass and their concentration in the rhizospheric soil. In maize, Fe was the element whose concentration in the soil increased as the Fe content extracted by the aerial part increased (r = 0.41 *). In wheat, as the zinc content in the aerial part of the crop increased, its concentration in the rhizospheric soil also increased (r = 0.44 *). Both Fe and Zn availability play an important role in the agroecosystem under study. For instance, according to Yong et al. [47], Zn plays a special role in soil ecology and fertility because it can support the growth of soil organisms or inhibit their growth depending on its concentrations.

4.2. Cover Crop Mixtures

There were no differences between the maize biomass with CC mixtures (B+V and B+M) and BAR (Table 5a). Therefore, the mixtures were not better than BAR in maize, and even they showed a lower percentage of colonization and a lower abundance of archaea and total fungi (rejection of hypothesis 3) (Figure 1a). This contrasts with some research that points out that crop mixtures based on complementary plant traits can increase the

multifunctionality of agroecosystems and produce higher crop yields [48]. In addition, it is often reported that mixtures provide more resources than monocultures to overcome important constraints such as diseases and pests [49]. However, in the absence of major constraints, the majority tendency is for monocultures to achieve higher yields [48].

Plant–plant interactions could explain the behaviors of CC mixtures that are divergent from those of their pure species [50], as was observed in Figure 1a and in other variables (Table 5). For example, B+M was able to export the highest amounts of Na from the soil to the maize and wheat plants, but none of the individual species in the mixture (BAR or VET) behaved in this way (Table 5a,b). Some researchers suggest that some glycosides may play a key role in Na transport in plants [51], and melilotus happens to produce at least one glucosinolate (Coumarins). This hormone is potentially alepotic [52], and its synthesis could probably be increased when melilotus was mixed with a potential competitor such as barley. We hypothesize that this secretion due to plant–plant interaction could indirectly affect Na^+ uptake in the subsequent maize and wheat crops (Table 5a,b).

4.3. Benefits of Cover Crop Residues on Biomass of Cash Crops

The mineralization of CC residues is directly related to their C:N ratio, which has effects on N recycling [53]. So legumes, with a lower C:N ratio compared to BAR [54], have a significantly higher decomposition rate than BAR and, within two to three weeks after termination, may have released 50% of their N [55]. In addition to the C:N ratio, there are other main factors that affect the rate of organic matter decomposition, such as temperature and soil moisture. Therefore, it is important to select a CC whose mineralization is as synchronized as possible with the nutrient demand of CaC in the rotations under study [56]. According to Perdigão et al. [57], in Mediterranean environments, the decomposition of both legume CC and certain CC grasses can favor the nutrition of subsequent CaC. In our case, maize after BAR was the treatment with the highest N, K, B, Mn, and Zn content extracted, which seems to confirm that BAR decomposition is well synchronized with maize demands under warm conditions and could be one of the reasons why BAR provided such good results with this CaC. All of which could be considered to reduce the amount of fertilizer that should be rationally applied to the agroecosystem. However, in other areas with slower mineralization, e.g., lower temperatures and/or more days of saturated soil, the decomposition of non-legumes residues may be out of step with the needs of maize [10]. To such an extent that non-legumes, being more efficient in N scavenging, may lead to a subsequent decrease in maize yield [10].

There was a positive and significant correlation between the biomass of CC and maize ($r = 0.49$ *). Thus, BAR, besides being the treatment that obtained the highest biomass of CC, was also the treatment that produced the highest aerial and root biomass of maize (Table 5a). This could be interpreted as a direct benefit of CC on maize production. Furthermore, we believe that the chopping and deposition of 100% of the CC residues on the soil were essential to obtaining these results [58].

However, the case of wheat was very different. All the CC that included barley (BAR, B+V, and B+M) impaired wheat biomass production compared to the control (Table 5b). Nielsen et al. [59] pointed out that this decrease in wheat productivity is common in semi-arid regions because CC water consumption is not usually replenished by rainfall at the time of CaC seeding. On the other hand, all CC with barley failed to comply with one of the CC selection rules: "Choose a CC that is broadly different from the next CaC" [60], because barley is of the same tribe as wheat (*Triticeae*). So, barley, on the one hand, consumes very similar resources and comes from an almost identical soil zone as wheat. On the other hand, barley could serve as a host for wheat-compatible pathogens [61]. In other words, planting CaC-like species in CC (whether in monoculture or in mixtures) can more or less subtly impair the subsequent CaC [21].

4.4. Relationship between Soil Microbiology and Nitrogen Content in Maize

Despite soil microbial variables being highly discriminating between treatments (Table 2a,b), no regression equations with $r^2 > 0.25$ were found to relate these to the biomass production of the CaC. Microbial variables can be modified relatively easily and show high spatial and temporal variability throughout a crop cycle [62]. Therefore, their high variability may be a weakness in determining, in a particular sampling, their relationship to key agroecosystem parameters such as, e.g., biomass production. Different from biomass, shoot N in maize was related to three microbial properties, such as bacterial abundance, archaeal abundance, and SIR (Equation (3)). In Equation (3), we saw that the total bacteria abundance negatively affected the N content of maize. Perhaps this was due to the ability and efficiency of bacteria to immobilize nitrate and thus decrease the nitrogen content extracted by maize [63].

Equation (3) also indicated that archaea increased the N content of maize. Archaea play a very significant role in plant development in environments with high abiotic stress, desiccation, and extreme temperatures, as sometimes occurred in the studied system [64]. According to Jung et al. [65], the role of archaea in nutrient cycling (as with N, C, P, and S) and siderophore production could provide nutrients that support and promote plant growth. In our study, archaeal abundance was correlated not only with N content (r = 0.44 *), but also with Mn content (r = 0.42 *) and Zn content in maize plants (r = 0.54 **). The direct correlation between archaea and Zn is of utmost importance, as Zn deficiency is one of the most common deficiencies in alkaline soils [66]. The specific mechanism that could have produced such a correlation is unknown, although perhaps some archaea have a mechanism to enhance Zn solubilization similar to that presented by *Gluconacetobacter diazotrophicus* [66].

4.5. Relationship between Maize Biomass and Soil Variables

Equation (1) selected the five soil variables (from Tables 3 and 4) that together were best related to maize biomass production.

(i) Firstly, increased penetration resistance is detrimental to maize biomass production because it impairs seed emergence and water/oxygen accessibility [67]. In our experiment, penetration resistance was not only negatively correlated with maize biomass production but also with biomass production in previous CCs (r = −0.58 ***, r = −0.48 **, respectively). Thus, penetration resistance informs efficiently on the potential of the soil for biomass production [68].

(ii) Secondly, we recall that Fe availability in carbonate soils is limited due to the formation of insoluble compounds such as Fe hydroxides and carbonates [69]. Thus, increasing Fe availability in these soils may improve maize biomass production, as indicated by Equation (1). However, none of the treatments studied was able to significantly increase soil Fe concentration.

(iii) As soil S increased, maize biomass increased. In addition, a positive correlation ($p < 0.01$) was found between soil S and previous CC biomass production, which reinforces the idea that S played a key role in biomass production. There are several reasons why S has this relevance. In our calcareous soil, a significant amount of sulphates (the assimilable form of S) is co-precipitated with $CaCO_3$ [70]. On the other hand, maize demands significant supplies of S due to its high requirements and sensitivity to S deficiency. Finally, and in the case of Europe, S fertilization needs have increased as inputs through atmospheric deposition or fertilizers have decreased substantially [71]. S concentrations in the maize soils of the CC mixtures were classified as very low or low (Table 4a) [72], but we did not find a satisfactory explanation for this last phenomenon.

(iv) Nitrogen is often the most limiting nutrient for maize development [73]. In our case, we applied low-nitrogen fertilization to all treatments. Therefore, maize biomass production was able to respond to small variations in available nitrogen, such as from the mineralization of the previous CC. Although legume-based CC (such as vetch and melilotus) are well known for their N fixation capacity [74], in the maize rotation, BAR was the treatment with the highest shoot N content (Table 5a). This could be due to the fact that barley and other grasses tend to be more efficient than legumes at capturing and replenishing aboveground residual N from the soil [10].

(v) Finally, as expected, soil pH affected the availability of most nutrients. In moderately alkaline soils, such as ours, the availability of most micronutrients (except for Mo) is seriously impaired [10,75]. Under these conditions, maize biomass increased with decreasing pH, as shown in Equation (1). It was also observed that the pH in maize soil (Table 3a) varied significantly depending on the treatment. According to Vives-Peris et al. [76], root exudates and respiration can change the pH of rhizospheric soil in order to solubilize nutrients and thus increase their availability. In addition, certain rhizosphere-associated soil microorganisms can also modify the pH of the surrounding soil [77].

However, in wheat, no satisfactory linear regression was obtained relating its biomass to soil nutrient concentrations. Moreover, no soil variable showed any significant correlation with wheat biomass. This could be because the heat stress suffered by wheat (with a mean temperature of 22.5 °C) was predominant and caused wheat biomass to be almost unresponsive to soil variables. The high temperatures also caused the results obtained to be very different from those obtained in the previous crop cycle, as can be seen, for instance, in the numerous differences between the PCA biplots of the microbial variables obtained in Ulcuango et al. [16] and those in Figure 1. Thus, the possible cumulative effects of CC after the second culture cycle were masked by the effects of the temperature increase [78].

4.6. Relationship between Maize Biomass and Plant Variables

Differences between the treatments were observed for most plant variables (Table 5). This confirmed the great effects that CC had on maize and wheat nutrition [79]. Linear regressions between CaC biomass and nutrient contents revealed that N and B played a crucial role in both maize and wheat biomass production (Equations (2) and (3)) (with a p-value < 0.001). Thus, N and B contents in shoots were able to explain the results of biomass with high reliability (Figure 2). In our experiment, the highest B contents in maize were obtained, once again, in the BAR treatment. Therefore, similar to what we discussed with N, we deduce that BAR was suitable for the cycling of B and its subsequent release into the soil in time to meet the needs of maize [80]. Finally, Ahmad et al. [81] indicate that B fertilization in soils deficient in B is very effective in increasing both maize and wheat biomass.

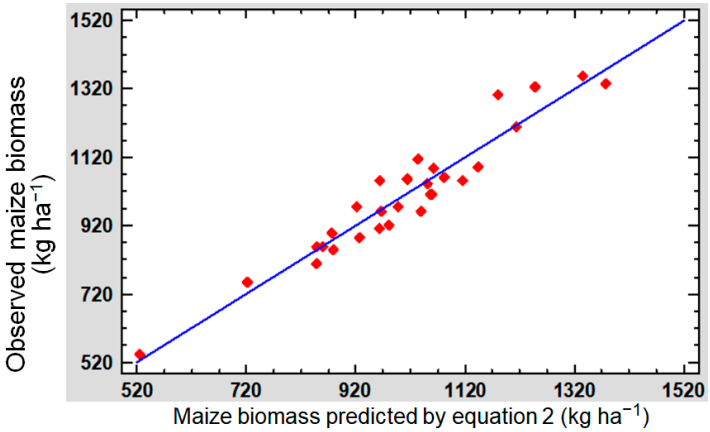


Figure 2. Maize biomass observations and their predictions according to the linear regression of Equation (2).

5. Conclusions

The different CCs and CaCs were able to shape the soil microbiome through their residues and exudates. Barley monoculture was the CC that showed the best results in maize under warm conditions because it provided the most residues and the highest shoot Ca, K, Mg, N, B, and Zn contents in maize. Additionally, BAR enhanced total fungi and AMF colonization compared to the control. In the rotation with maize, BAR also stood out for its high abundance of archaea, which play a key role in soils under significant thermal stress. Archaea also showed a high correlation with plant Zn content, which is of utmost importance as Zn deficiency is one of the most common micronutrient deficiencies in alkaline soils. However, the specific mechanism that could have produced such a correlation is unknown, although we hypothesized that some archaea were able to facilitate Zn availability. In wheat, the heat stress seems to have resulted in the absence of a biomass response to soil variables. CC mixtures did not prove to be better than BAR in maize or than MEL in wheat.

The selected CC should be as different as possible from the CaC. In particular, the use of barley in CC (as monoculture or in mixtures) just before wheat should be avoided. This study confirms the relationship between B and CaC and, therefore, the significance of the effects of CC on B. Specific research is needed to explain the main microbial mechanisms governing these results in order to select, in each case, the CC whose mineralization is in step with the needs of the next CaC and also stimulates plant growth-promoting microorganisms.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/agronomy13071721/s1, Table S1. A primer set was selected for the quantification of the main groups of microorganisms evaluated in this study. Table S2. Selected properties at the end of the cover crops in the rotations with (a) maize and with (b) wheat. Figure S1. Principal component analysis biplot of macro and micro nutrients and confidence ellipses of each treatment in (a) maize shoots and in (b) wheat shoots.

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Data Availability Statement: The datasets generated during and/or analyzed during the current study are available from the corresponding authors on reasonable request.

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