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RESEARCH

Response of broiler chickens to dietary different yeast cell wall components challenged with *Salmonella typhimurium*

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Abstract

This study assessed the impact of dietary prebiotic supplementation on broiler chickens challenged with *Salmonella Typhimurium*. In experiment I, the treatments consisted of control (K) [without supplementation]; supplemented with 0.565% autolyzed whole yeast cell (W); supplemented with 0.125% autolyzed whole yeast cell (WP); supplemented with 0.565% enzymatically removed yeast cell wall (CELL) and supplemented with 0.2% pure Mannan-oligosaccharides (MOS) + β-glucan (MB). The second experiment, the *Salmonella Typhimurium* challenge was performed on day 7 post-hatch. Birds in the CELL group in Experiment I exhibited higher final body weight and weight gain ($P=0.001$). On day 21, jejunum villus height (VH) was lower in the MB group, while jejunum crypt depth (CD) was lower in the WP and K groups *(*$P<0.05$). The W group had the lowest VH and CD in the ileum ($P<0.05$). At day 35, jejunal villus health was unaffected by prebiotic supplementation, but the CELL group showed the highest VH and CD in the ileum ($P<0.05$). Gene expression analysis revealed significant differences in claudin, IL-1β, and IL-10 expressions. In experiment II, the CELL group exhibits the highest final live body weight and weight gain ($P<0.05$). Intestinal histology varied among groups and time points. Gene expression analysis indicated upregulation of claudin and occludin in certain groups, while IL-1β was upregulated in all groups and IL-10 showed varied expressions. In conclusion, prebiotic supplementation, particularly yeast cell wall, positively influenced broiler performance, intestinal histology, and gene expression related to the intestinal barrier.

Keywords Prebiotic · Short chain fatty acids · B-glucan · Broiler

Introduction

Salmonellosis is a costly disease in poultry production, leading to significant reductions in productivity (Aljumaah et al. 2020). It is a foodborne disease transmitted to humans through contaminated meat processing and consumption (Abudabos et al. 2017). Young chicks are particularly susceptible to *Salmonella* infection due to their weakened immune system and rapid growth (Abudabos et al. 2019). *Salmonella* can rapidly proliferate in the intestinal tract of a bird once introduced into its body, resulting in stunted growth, severe morbidity, and mortality (Khan and Naz 2013). *S. Typhimurium*, an infectious serotype in chickens, can cause salmonellosis in humans (Gopinath et al. 2012). To control this infection, antibiotics and vaccines are commonly used as preventative measures (Bajpai et al. 2012).

The removal of antimicrobial growth promoters from poultry diets has resulted in an increase in the risk of pathogenic infection and consequently reducing poultry production levels. Thereby, applied strategies including vaccines and alternative feed additives for antibiotics are important to control the infections and to keep poultry production at a reasonable level (Shao et al. 2016; Ahmad et al. 2020). One such alternative is prebiotics that could potentially compete

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with antimicrobial growth promoters and sustain the growth of poultry industry (Abd El-Hack et al. 2022). Prebiotics are non-digestible compounds such as Mannan-oligosaccharides (MOS) and β-glucans that have a positive impact on the host by modifying the composition and metabolism of the gut microbiota (Abd El-Hack et al. 2020a; Alagawany et al. 2020). Recently, prebiotics administration has been shown to reduce pathogens and improve broilers growth performance in various trials (Froebel et al. 2019). In this context, administration of MOS alone or in combination with β-glucans enhanced immune system and histomorphology of gut (Morales-López et al. 2009a) and decreased *Salmonella* counts in laying hens (Jahanian and Ashnagar 2015).

The structure of yeast cell wall (YCW) *Saccharomyces cerevisiae* is composed of the β-glucan and MOS which are covalently linked to form macromolecular complexes. The activity of these complexes varies due to different methods containing enzyme hydrolytic process and autolysis used to prepare the product. This variation might be the reason for different effects outcomes that have been reported in the trials when using YCW as a prebiotic feed additive (Legras et al. 2007).

We hypothesized that different preparations of YCW added into broilers diets might improve performance, histomorphological parameters of intestine wall; enhance gene expression of tight junction proteins and cecal tonsils towards *Salmonella* infection. With this aim, the objectives of the following studies were to determine the influence of dietary MOS and β-glucan especially removed from links of YCW alteration on performance parameters, intestinal morphology, and expression of occludin and claudin, internal organs weight, IL-1β and IL-10 gene in broilers following oral *S. Typhimurium* challenge. By detailing improvements in intestinal morphology and clarifying the immunomodulatory effects through gene expression analysis of tight junction proteins (occludin, claudin) and immune-related cytokines (IL-1β, IL-10), the research offers crucial insights into boosting gut health and resilience against pathogens. These findings are pivotal for future applications in developing targeted nutritional strategies, formulating functional feeds to reduce reliance on antibiotics, and guiding further in-depth mechanistic studies to optimize poultry production and food safety.

Materials and methods

Animal management, diets and experimental design

In Experiment I, a total of 320, 1-day old Ross 308 male broilers obtained from a local hatchery (Beypiliç A.Ş., Turkey) were weighted and randomly assigned to five groups with eight subgroups (8 birds/pen). The basal diet was formulated with standard broiler diet for multiple stages (starter, grower, and finisher) based on the Ross catalogue and offered in mash form. The control group (K) received the basal diet without supplementation. Other groups were supplemented as follows: autolyzed whole yeast cell at 0.565% (W), autolyzed whole yeast cell at 0.125% (WP), yeast cell wall (CELL) with enzymatic bond removal at 0.565%, and powdered form of pure MOS + β-glucan at 0.2% (MB) (Table 1). The supplementation for each treatment was performed throughout the entire grow-out period.

In Experiment II, a total 200 male broiler chickens (Ross 308) were used. Dietary treatments were formulated like experiment I. There were four replicate cages of all groups with ten birds per cage. For Experiment I, the grow-out period spanned 42 days, while Experiment II had a shorter 35-day grow-out. In both experiments, the pen was designated as the experimental unit.

Bacterium challenge

The avian pathogenic *Salmonella* enterica serovar Typhimurium was isolated from naturally infected commercial broilers. The isolated strain was characterized phenotypically identified and also identified genotypically by 16 S rRNA gene sequencing method (Shen et al. 2023).

Pure cultures of bacteria were resuspended in 20% (v/v) glycerol stocks. Bacteria were cultured on nutrient broth (Oxoid, Germany) for 24 h at 37 °C, then sub-cultured on Xylose Lysine Deoxycholate (XLD) agar (Oxoid, Germany) at 37 °C for 24 h. To determine the concentration of

Table 1 Physical and chemical composition of the basal diet

Feedstuffs (g/kg)	Starter	Grower	Finisher
Corn	566.00	598.30	595.30
Soybean meal	359.50	331.00	341.50
Oil	40.00	38.00	30.50
Limestone	5.00	5.00	5.00
DCP	16.50	14.55	14.55
Methionine	2.20	2.35	2.35
Lysine	3.30	3.30	3.30
Threonin	1.50	1.50	1.50
Salt	3.50	3.50	3.50
Vitamin	1.00	1.00	1.00
Mineral	1.00	1.00	1.00
Choline chloride	0.50	0.50	0.50
Chemical composition (Calculated)			
CP, %	21.05	20.85	20.05
ME, kcal/kg	3050	3150	3215
Ca, %	0.96	0.94	0.90
P, %	0.48	0.44	0.40
Lysine, %	1.41	1.30	1.21
Methionine, %	0.54	0.53	0.53

viable *Salmonella* Typhimurium, the pure culture was centrifuged at 5,000 g for 15 min, and the pellet was washed three times and diluted in sterile PBS (pH 7.2). Bacterial counts were then adjusted to approximately 1×10^8 CFU/ml using McFarland dansitometer (Biosan, Latvia) (Tarabees et al. 2023).

Salmonella challenge was performed by individual oral administration of 1 ml 3×10^8 cfu/ml *Salmonella Typhimurium* at the 7th day post-hatch for all groups in experiment II. On day 14 of age (on the 7th day of infection), two chicks from each trial group were taken and both ceca were ligated and removed aseptically from the gastrointestinal tract and stored at −20 °C for Salmonella spp counts by real time PCR analysis(Shao et al. 2013).

Broiler performance

To evaluate the growth performance of broiler chicks (in both experiments), feed intake was recorded, and average daily feed intake was calculated. Also, live body weight was recorded at weekly intervals to obtain average weight gain. While the total feed intake and final body weight were recorded at the end each feeding trail. The feed conversion ratio (FCR) was calculated for each group by using body weight gain and feed consumption values.

Internal organs

In experiment I, following the slaughter on day 42 post hatching, one median weight bird in each cage was selected, and liver, spleen, gizzard, proventriculus, heart, bursa of Fabricius was removed and weighed. In experiment II, on the 35th day, the median weight of two birds in each sub-group were selected and internal organ weights determined.

Histomorphology analysis of the gut wall

Experiment I, one bird (while two birds in experiment II) from each subgroup were taken randomly at days 21 and 35 post hatching, weighed individually and slaughtered. Ileum and jejunum segments (midway between the point of entry of the bile ducts and Meckel's diverticulum, approximately 1 cm) were immediately removed, rinsed with physiological saline, and fixed in 10% formalin, processed by the routine paraffin sectioning, and finally blocked in paraplast and cut into 6 µm thick sections for histomorphological analysis described previously (Chen et al. 2016). Measurements of villus height (VH) were selected from sections in which the villus tops were well oriented and adjacent to crypt mouth. The crypt depth (CD) from the crypt mouth to the base was also measured. Results were evaluated by using the Image J analysis software.

Quantitative PCR (qPCR) for measuring intestinal barrier related gene levels in jejunum, ileum and cecal tonsil

On the 35th day in both Experiments 8 birds in each group were selected, euthanized, and jejenum, ileum and cecum tissues were excised and snap-frozen in liquid nitrogen to later assess the mRNA abundance of target genes. Tissues were homogenized in TRI Reagent (Zymo Research, Irvine, CA) using a Tissue Lyser II (Qiagen, Valencia, CA). Total RNA was extracted using the Direct-zol RNA Miniprep Plus Kit (Zymo Research, Irvine, CA), and was measured at 260 nm for its concentration and purity using Epoch™ Microplate Spectrophotometer (Biotek, VT, USA). First-strand cDNA was performed using the High Capacity cDNA Reverse Transcription Kit (Applied Biosystems, Foster City, CA) and the cDNA was stored at −20 °C.

Quantitative Real-Time PCR

Real-time PCR was performed for the specified genes and β-actin Messenger RNA (mRNA) expression quantitatively; a real-time PCR was performed using Qıaigen Rotorgene. The qRT-PCR was conducted using a Power SYBR Green PCR Master Mix to assess analyses gene expression. Data about the primer sequences for both the target genes and B actin as the housekeeping gene used in the study are given in supplementary Table 2. The following thermal cycling conditions were applied to all samples as follows: an initial denaturation at 95 °C for 15 min, followed by 40 cycles at 95 °C for 15 s and, annealing at 60 °C for 20 s following and an extension period at 72 °C for 20 s. Each experiment sample was carried outrun with each sample in triplicate. The β-actin gene was used as the housekeeping gene to quantify the relative expression levels of the target genes by using $2^{-\Delta\Delta Ct}$ method genes were normalized to the mRNA level of the β-actin gene. The $2^{-\Delta\Delta Ct}$ method was used to quantify the relative expression levels of the genes of interest. The calibrator for each gene was the average ΔCt value from control group.

Statistical analysis

Statistical analyses were performed using SPSS 14.01 program (SPSS Inc. Chicago, IL, USA). The data were analyzed using a one-way analysis of variance (ANOVA) test followed by Duncan test. $P \leq 0.05$ was declared to be significant for all the comparisons. The data are presented as the standard error mean.

Table 2 The effects of treatments on feed intake, body weight and feed conversion ratio of non-infected broiler (from day 1-42)

Parameters	Treatments[1]					SEM[2]	*P* value
	K	W	WP	CELL	MB		
Feed intake (g)	3777	3857	3825.25	3913.38	3813.375	25.54	0.54
Initial body weight (g)	43.47	43.55	43.36	43.21	43.32	0.11	0.874
Final body weight (g)	2396.75	2467.88	2448.375	2541.5	2432.125	12.06	0.001
Final weight gain (g)	2353.16	2424.32	2404.97	2498.22	2388.87	12.06	0.001
Feed conversion ratio	1.61	1.59	1.59	1.57	1.60	0.01	0.761

[1]Basal diet without supplementation (K); supplemented with 0.565% autolyzed whole yeast cell (W); supplemented with 0.125% autolyzed whole yeast cell (WP); supplemented with 0.565% yeast cell wall that removed the bond with enzymatic reactions (CELL) and supplemented with 0.2% pure MOS + β-glucan (MB) in powdered form all

[2]The standard error of mean

Table 3 Mean weight (g) and relative weight (%) of different non-infected broiler carcass parts for each treatment

Parameters	Treatments[1]					SEM[2]	*P* value
	K	W	WP	CELL	MB		
Carcass (g)	1786.8^{ab}	1618.2^{b}	1611.0^{b}	1922.0^{a}	1751.4^{ab}	34.13	0.009
Liver (g)	47.93^{ab}	48.13^{ab}	40.74^{c}	51.70^{a}	42.70^{bc}	1.12	0.004
Spleen (g)	3.54	3.26	3.15	3.65	2.56	0.18	0.376
Bursa Fabricius (g)	4.89	4.38	4.84	5.01	3.87	0.24	0.558
Gizzard (g)	40.32	41.68	40.59	39.92	47.38	1.14	0.203
Proventriculus (g)	10.72	10.92	10.69	10.43	12.23	0.37	0.607
Abdominal fat (g)	19.59	20.67	17.34	13.09	21.53	1.23	0.191
Heart (g)	13.65^{ab}	13.54^{ab}	11.54^{b}	15.76^{a}	13.06^{b}	0.43	0.024
Relative weight (%)							
Carcass	69.35^{c}	69.29^{c}	70.88^{abc}	71.99^{ab}	71.19^{abc}	0.35	0.035
Liver	1.86^{ab}	2.06^{a}	1.80^{b}	1.95^{ab}	1.73^{b}	0.04	0.037
Spleen	0.11	0.14	0.11	0.14	0.08	0.01	0.318
Bursa of Fabricius	0.19	0.19	0.22	0.15	0.16	0.01	0.433
Gizzard	1.58^{abc}	1.79^{ab}	1.80^{ab}	1.52^{bc}	1.92^{a}	0.06	0.147
Proventriculs	0.42	0.47	0.47	0.39	0.5	0.01	0.32
Abdominal fat	0.77^{abc}	0.88^{a}	0.76^{abc}	0.49^{bc}	0.87^{a}	0.05	0.104
Heart	0.53	0.58	0.51	0.59	0.53	0.01	0.324

[1]Basal diet without supplementation (K); supplemented with 0.565% autolyzed whole yeast cell (W); supplemented with 0.125% autolyzed whole yeast cell (WP); supplemented with 0.565% yeast cell wall that removed the bond with enzymatic reactions (CELL) and supplemented with 0.2% pure MOS + β-glucan (MB) in powdered form all

[2]The standard error of mean

Results

Experiment I

Performance parameters, carcass traits and relative weight of some internal organs

The total feed intake did not differ between the experimental groups (Table 2). The data revealed that birds of fed CELL group were heavier than other groups ($P=0.001$). In addition, the same group showed the highest weight gain compared to the control group ($P=0.001$). On the other hand, the FCR was not affected by dietary supplementation ($P=0.761$).

The supplementation of prebiotics increased dressing weight ($P=0.009$) and dressing percentage ($P=0.03$) (Table 3). Moreover, dressed weight was higher ($P<0.05$) in CELL group compared W and WP groups and eviscerated carcass as a percentage of the body weight was greater for broilers in the CELL group than those receiving control and W diets. Except for liver ($P=0.004$) and heart ($P=0.024$) weights, the dietary supplementations had no effect on internal organs weight. The birds in CELL group showed higher liver and heart weight compared to birds in the WP and MB groups ($P<0.05$). The relative weight of the liver was the greatest for broilers fed W diet ($P=0.037$) while relative weight of abdominal fat was higher in carcass of birds fed W and MB diets than birds fed CELL diet.

Intestinal istological features

On day 21, VH was lower in the Jejunum of MB and WP groups while CD was higher in the jejunum of WP and CELL groups and lower in MB group ($P<0.05$, Table 4).

Table 4 The effects of treatments on villi height (VH), and crypt depth (CD) of non-infected broiler (21 and 35 day)

Treatments[1]	Day 21						Day 35					
	Jejenum			Ileum			Jejenum			Ileum		
	VH[2]	CD[3]	VH/CD	VH[2]	CD[3]	VH/CD	VH[2]	CD[3]	VH/CD	VH[2]	CD[3]	VH/CD
K	1084.31^{ab}	173.88^{b}	6.30	858.00^{ab}	136.44^{abc}	6.31	1346.25	172.58	7.87	1109.00^{ab}	149.08^{b}	7.45
W	1133.13^{ab}	181.31^{ab}	6.28	838.00^{b}	125.94^{c}	6.68	1235.92	158.33	7.85	1105.92^{ab}	141.08^{bc}	7.86
WP	1044.69^{b}	180.75^{ab}	5.81	925.44^{a}	144.69^{ab}	6.41	1224.92	158.25	7.76	1079.83^{bc}	133.33^{c}	8.16
CELL	1177.75^{a}	195.81^{a}	6.03	934.25^{a}	149.00^{a}	6.31	1362.83	181.25	7.55	1165.08^{a}	161.83^{a}	7.22
MB	1034.50^{b}	167.21^{b}	6.20	898.88^{ab}	131.69^{bc}	6.83	1283.33	168.08	7.64	1157.83^{ab}	141.42^{bc}	8.19
SEM[4]	17.20	2.51	0.12	12.31	2.39	0.08	29.16	3.93	0.13	15.86	2.31	0.15
P value	0.137	0.041	0.663	0.045	0.008	0.100	0.473	0.298	0.947	0.392	0.0001	0.136

[1]Basal diet without supplementation (K); supplemented with 0.565% autolyzed whole yeast cell (W); supplemented with 0.125% autolyzed whole yeast cell (WP); supplemented with 0.565% yeast cell wall that removed the bond with enzymatic reactions (CELL) and supplemented with 0.2% pure MOS+β-glucan (MB) in powdered form all

[2] Villi height

[3]Crypt depth

[4] The standard error of mean

The ileum of birds in W group showed the lowest VH and CD ($P<0.05$). On day 35, neither VH or CD or their ratio were affected by dietary treatments in jejunum while the ileum of birds in CELL group showed the highest VH and CD ($P<0.05$).

Intestinal barrier related gene levels in jejunum, ileum and cecal tonsil

The effects of treatments on intestinal barrier related gene level at different intestinal parts were expressed in Fig. 1 (A, B, C). Analysis of gene expression levels of claudin, IL1β, and IL-10 revealed significant differences between the experimental groups ($P<0.05$). Compared to K, the expression of claudin was upregulated in the CELL group by 0.3-fold, in the MB group by 0.5-fold, and downregulated in the W group by 0.6-fold ($P<0.05$). The expression of IL-1β was upregulated in the CELL group by 1.2-fold, downregulated in the MB and WP groups by 0.6 and 0.75 -fold respectively, and further downregulated in the W group by 0.9-fold compared to control. The expression of IL-10 was upregulated in the CELL group by 4.5-fold, in the MB group by 3.6-fold, in the WP group by 2.4-fold, and in the W group by 1.8-fold, while it remained unchanged in the control group.

Experiment II

Performance parameters, carcass traits and relative weight of some internal organs

The feed intake was highest in the WP treatment and lowest in the control group, but the difference was not statistically significant ($P=0.932$), and initial live weight did not differ among groups ($P=0.975$). While final live body weight was highest in the CELL group and lowest in the control group, but the difference was not significant ($P=0.285$). The final weight gain was highest in the CELL group and lowest in the K group ($P<0.05$). The FCR was lowest in the WP and CELL groups, but the difference was not significant (Table 5).

Carcass, liver, and spleen weight did not differ significantly among treatments (Table 6). Bursa of Fabricius weight was the highest in the W group and lowest in the WP group ($P<0.05$). On the other hand, the gizzard weight was the highest in the K group and lowest in the MB group, and relative gizzard weight followed the same pattern ($P<0.05$). The proventriculus weight showed significant differences among the treatments, with the highest weight in the W group and lowest in the CELL group ($P<0.05$), and the proventriculus relative weight was highest in the K and W groups and lowest in the CELL treatment ($P<0.05$).

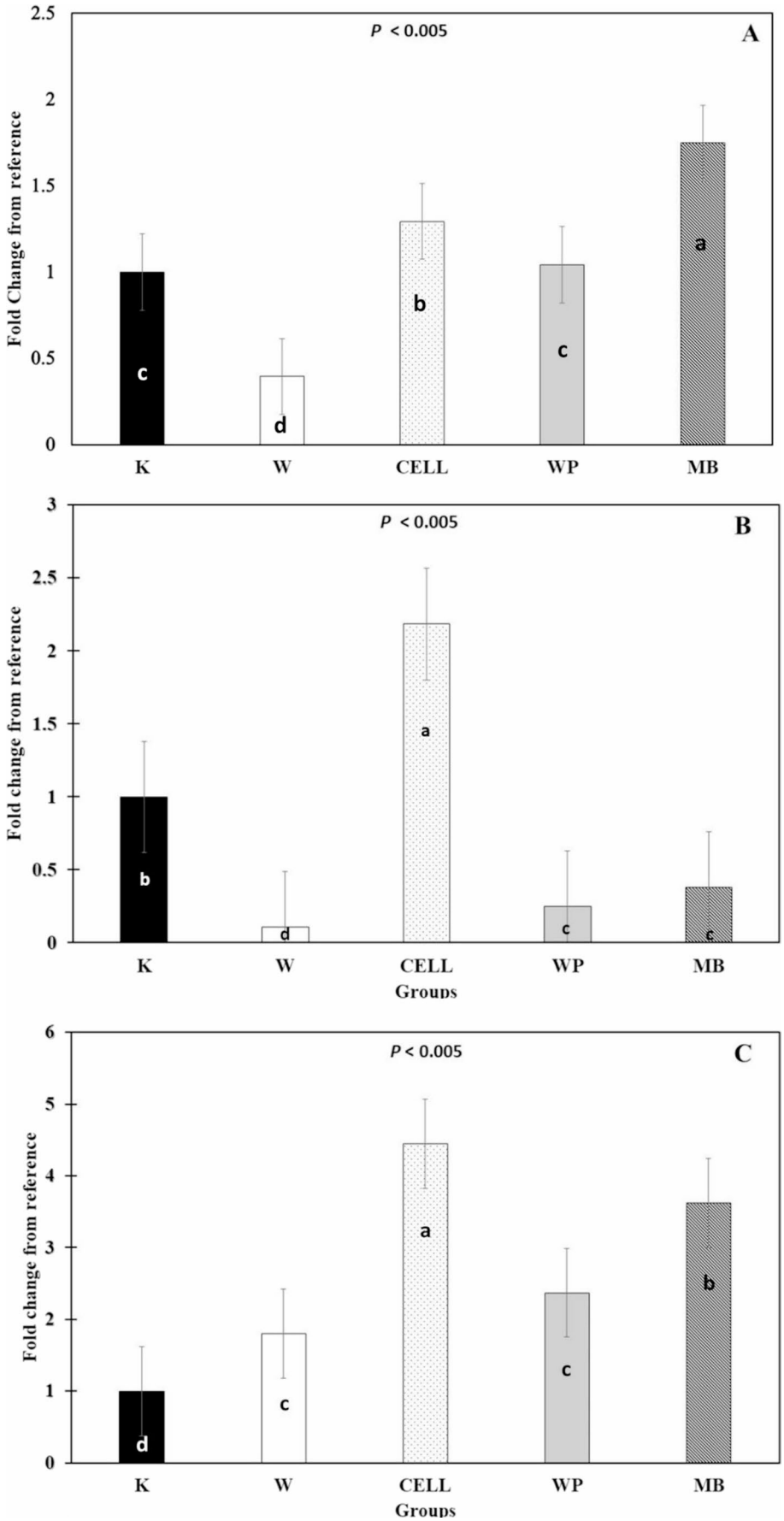


Fig. 1 Intestinal barrier related gene level at different intestinal parts of healthy broilers fed different diets, K (basal diet without feed additive); W (basal diet supplemented with 0.565% autolyzed whole yeast cell); WP (basal diet supplemented with 0.125% autolyzed whole yeast cell; CELL (basal diet supplemented with 0.565% yeast cell wall that removed the bond with enzymatic reactions) and MB (basal diet supplemented with 0.2% pure MOS + β-glucan. **A** claudin in jujenum, (**B**) IL1β in cecal tonsill and (**C**) IL10 jujenum

Table 5 The effects of treatments on feed intake, body weight and feed conversion ratio of *Salmonella* infected broiler (from day 1-35)

Parameters	Treatments[1]					SEM[2]	*P* value
	K	W	WP	CELL	MB		
Feed intake (g)	3108	3180	3107	3181	3129	33.58	0.932
Initial body weight (g)	41.85	42.03	41.85	42.05	41.88	0.12	0.975
Final body weight (g)	1999	2088	2098	2147	2099	21.36	0.285
Final weight gain (g)	1957^{b}	2047^{ab}	2056^{ab}	2105^{a}	2058^{ab}	21.41	0.288
Feed conversion ratio	1.59	1.55	1.51	1.52	1.54	0.02	0.710

[1]Basal diet without supplementation (K); supplemented with 0.565% autolyzed whole yeast cell (W); supplemented with 0.125% autolyzed whole yeast cell (WP); supplemented with 0.565% yeast cell wall that removed the bond with enzymatic reactions (CELL) and supplemented with 0.2% pure MOS + β-glucan (MB) in powdered form all

[2]The standard error of mean

Table 6 Mean weight (g) and relative weight (%) of different *Salmonella* infected broiler carcass parts for each treatment

Parameters	Treatments[1]					SEM[2]	*P* value
	K	W	WP	CELL	MB		
Carcass (g)	2046.75	2157.75	1988.88	2158.75	2069.00	40.01	0.628
Liver (g)	36.68	35.30	36.67	38.99	40.45	1.02	0.529
Spleen (g)	1.57	1.81	1.44	1.68	1.63	0.08	0.717
Bursa Fabricius (g)	4.05^{ab}	5.14^{a}	3.49^{b}	4.33^{ab}	4.09^{ab}	0.18	0.037
Gizzard (g)	34.08^{a}	29.10^{b}	25.93^{bc}	26.68^{bc}	23.68^{c}	0.92	0.002
Proventriculus (g)	8.69^{ab}	9.50^{a}	7.85^{bc}	7.46c	8.11^{bc}	0.20	0.006
Heart (g)	10.72^{ab}	12.65^{a}	10.16^{b}	11.93^{ab}	10.53^{ab}	0.34	0.089
Relative weight (%)							
Liver	1.79	1.64	1.84	1.81	1.97	0.04	0.102
Spleen	0.08	0.09	0.07	0.08	0.08	0.00	0.928
Bursa Fabricius	0.20	0.24	0.18	0.20	0.17	0.001	0.101
Gizzard	1.67^{a}	1.52^{ab}	1.32^{bc}	1.24^{bc}	1.17^{c}	0.06	0.017
Proventriculs	0.43^{a}	0.44^{a}	0.40^{ab}	0.35b	0.40^{ab}	0.09	0.006
Heart	0.53	0.59	0.52	0.55	0.51	0.02	0.398

[1]Basal diet without supplementation (K); supplemented with 0.565% autolyzed whole yeast cell (W); supplemented with 0.125% autolyzed whole yeast cell (WP); supplemented with 0.565% yeast cell wall that removed the bond with enzymatic reactions (CELL) and supplemented with 0.2% pure MOS + β-glucan (MB) in powdered form all

[2]The standard error of mean

Intestinal histological features

On day 21, in the jejunum, the CELL and MB groups had higher VH ($P<0.05$) compared to the control (Table 7). The CD value was higher in the CELL group compared to the control group which exhibits the lowest CD value ($P<0.05$). In the ileum, the VH values were higher in the WP group compared to the control group ($P=0.019$), while the W and K treatments had lower VH values compared to the other treatments ($P<0.05$). The CD values were higher in the MB group compared to the other treatments ($P<0.05$). The VH/CD ratio was highest in the WP group and lowest in the MB group. On day 35, in the jejunum, the VH values ranged from 1140.25 to 1225.38, with the highest value observed in the K group and the lowest value observed in the CELL group, yet no significant difference was observed ($P=0.441$). The CD values showed significant differences among the treatment groups ($P<0.05$), with the WP group exhibiting the highest value and the control group the lowest. In the ileum, there were no significant differences in VH between the treatment groups ($P=0.392$). Similarly, CD did not differ significantly across the treatment groups in the ileum ($P=0.18$).

Intestinal barrier related gene levels in jejunum, ileum and cecal tonsil

In the W group, the expression of claudin was upregulated by 0.1-fold compared to the control group ($P<0.05$). In the CELL group, the expression was upregulated by 1.2-fold compared to the control group. In the WP group, expression was upregulated by 0.5-fold compared to the control group. In the MB group, the expression was significantly upregulated 1.7-fold compared to the control group (Fig. 2A).

The expression of occludin in the jejunum of infected birds was shown in. In the control group, the expression was considered as the reference with a fold change of 1. Interestingly, in the W group, there was a slight upregulation with a fold change of 1.03 compared to the control

Table 7 The effects of treatments on villi height (VH), and crypt depth (CD) of *Salmonella* infected broiler (21 and 35 day)

Treatments[1]	Day 21						Day 35					
	Jejenum			Ileum			Jejenum			Ileum		
	VH[2]	CD[3]	VH/CD	VH[2]	CD[3]	VH/CD	VH[2]	CD[3]	VH/CD	VH[2]	CD[3]	VH/CD
K	990.25^{bc}	104.0^{c}	9.5^{ab}	714.19	100.06^{b}	7.15	1225.38	118.31^{b}	10.38^{a}	862.44	103.81	8.5
W	1052.44^{ab}	106.75^{bc}	9.85^{a}	714.19	100.06^{b}	7.15	1206.38	132.06^{a}	9.15^{b}	888.81	111.38	8.05
WP	1075.81^{ab}	113.56^{b}	9.50^{ab}	746.63	100.00^{b}	7.5	1189.81	135.25^{a}	8.81^{b}	906.06	109	8.4
CELL	1099.00^{a}	125.19^{a}	8.81^{b}	710.5	97.44^{b}	7.32	1140.25	130.31^{a}	8.79^{b}	952.31	114.5	8.33
MB	1102.44^{a}	107.06^{bc}	10.32^{a}	744.06	111.31^{a}	6.68	1148	127.75^{ab}	8.99^{b}	878.69	99.5	8.82
SEM[4]	15.70	1.67	0.15	0.15	15.59	1.61	16.78	1.80	0.15	15.01	2.15	0.16
P value	0.14	0.001	0.019	0.019	0.50	0.002	0.441	0.027	0.002	0.392	0.18	0.687

[1]Basal diet without supplementation (K); supplemented with 0.565% autolyzed whole yeast cell (W); supplemented with 0.125% autolyzed whole yeast cell (WP); supplemented with 0.565% yeast cell wall that removed the bond with enzymatic reactions (CELL) and supplemented with 0.2% pure MOS+β-glucan (MB) in powdered form all

[2] Villi height

[3]Crypt depth

[4] The standard error of mean

group ($P<0.05$). However, in the CELL group, there was an upregulation with a fold change of 8.2 from the reference ($P<0.05$). Similarly, in WP and MB groups, there was also a substantial upregulation with fold changes of 9.93 and 9.5 respectively compared to the control group (Fig. 2B).

The results of expressions of IL-1β and IL-10 were expressed in Fig. 2 (C and D, respectively). In the W group, the expression of IL-1β was upregulated, with a fold change of 4.23 compared to the control group ($P<0.05$). Similarly, in the CELL group, the expression of IL-1β was slightly upregulated, with a fold change of 1.74 compared to the control group. In the WP group and the MB group, there was also a modest upregulation of IL-1β expression, with fold changes of 1.97 and 2.28, respectively ($P<0.05$).

In contrast, the expression of IL-10 showed more complex results. In the W group, there was an upregulation of IL-10 expression, with a fold change of 3.73 compared to the control group. In the CELL group, there was also an upregulation of IL-10 expression, with a fold change of 2.85 compared to the control group ($P<0.05$). However, in the WP group and the MB group, the expression of IL-10 was downregulated, with fold changes of 0.98 and 0.84, respectively ($P<0.05$).

Discussion

Intensive farming systems in the livestock industry, implemented to meet the high demands for meat and milk, can inadvertently facilitate the transmission of bacterial diseases. These systems often exhibit low genetic diversity and high stocking density, which contributes to the occurrence of simultaneous production and economic losses (Jones et al. 2013). Dietary supplementation of YCW has been discovered to confer various beneficial effects, including the reduction of pathogenic bacteria, promotion of immunoglobulin production, prevention of diseases through pro-inflammatory responses, and modification of the composition of gut microbiota in both healthy and *S. Typhimurium*-challenged broilers (Ahiwe et al. 2020; Pascual et al. 2020). However, the effects of YCW on broiler performance and health have been inconsistent in research, likely due to differences in the specific *S. cerevisiae* strains, substrates (such as wine, beer, and bread), fermentation conditions and yeast cultivation techniques used, which can impact the composition of YCW fractions like MOS and β-glucans. Additionally, variations in experimental design, including trial length and the presence or absence of specific challenges and stressors, may contribute to the inconsistent findings.

Adding hydrolyzed yeast led to enhanced antioxidant potential, along with improved resistance against diseases

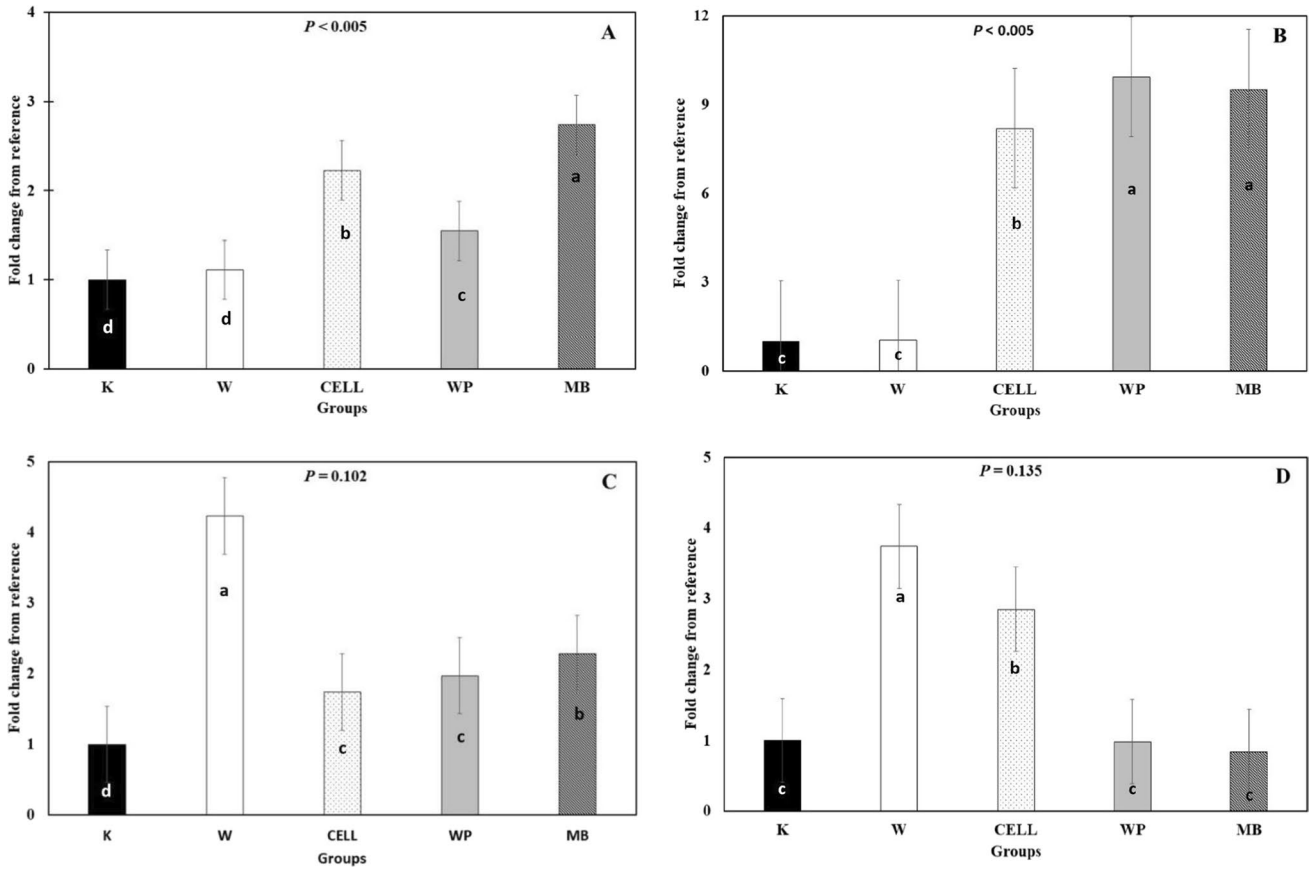


Fig. 2 Intestinal barrier related gene level at different intestinal parts of *Salmonella* challenged broilers fed different diets, K (basal diet without feed additive); W (basal diet supplemented with 0.565% autolyzed whole yeast cell); WP (basal diet supplemented with 0.125% autolyzed whole yeast cell; CELL (basal diet supplemented with 0.565% yeast cell wall that removed the bond with enzymatic reactions) and MB (basal diet supplemented with 0.2% pure MOS + β-glucan. **A** claudin in jujenum, (**B**) occludinn in jujenum(**C**) IL1β in cecal tonsill and (**D**) IL10 jujenum

and enhanced general immune responses in aquatic organisms (Jin et al. 2018; Andriamialinirina et al. 2020). This implies that integrating enzymatically treated yeast into animal production holds significant promise and potential. Nonetheless, prevailing research on hydrolyzed yeast has predominantly focused on ruminants, pigs, or aquatic animals. Among the prebiotics used, supplementation with 0.565% yeast cell wall that removed the bond with enzymatic reactions (CELL) resulted in the highest weight gain and dressed weight of broiler chickens. These findings agreed with Wang et al. (2022) who reported that dietary hydrolysate yeast beneficially improves carcass traits and relative organ weight. The improvement in dressed weight and dressing percentage suggests enhanced meat yield (Zhang et al. 2022). The CELL group displayed a notable escalation in liver weight, serving as an indication of enhanced metabolic capacities, in comparison to the W and MB groups. This implies that the disparities in growth between the CELL group and the other groups can be attributed to variations in nutrient metabolism.

The capacity of an animal's lymphoid organ to produce lymphoid cells during an immune response is indicated by the organ's size. Consequently, compromised immune systems are associated with smaller lymphoid organs. The spleen plays a critical role in blood filtration, pathogens clearance, and the promotion of adaptive immune cell growth and maturation. The bursa of Fabricius is a key lymphoid organ in poultry that is critical for B-lymphocyte differentiation (Haley 2017). The effect of supplementary yeast on lymphoid organ development varies. Some studies have reported that feeding various forms and doses of yeast products enhanced lymphoid organ weights (Zhang et al. 2008; Morales-López et al., 2009a), while others found no significant effects (Rathgeber 2011).

The VH, CD, and VH: CD ratio can be used to gauge an animal's intestinal morphology and overall health (Montagne et al. 2003; Zhang et al. 2008). An increase in jejunal VH at day 21 in CELL fed broiler chickens suggesting improved nutrient absorption potential and lower CD in the

W, WP, and MB groups indicating a potential reduction in cellular turnover which indicates a contributing role in gut health (Alagbe et al. 2023). At day 35, the observed variations in VH and CD in the jejunum and ileum suggest that the different treatments continued to affect the intestinal morphology however, the effect was more prominent on ileum. The differential effects of prebiotics on ileum and jejunum VH and CD in broilers fed different prebiotics at different ages (day 21 and 35) can be attributed to combination of factors related to developmental stage, prebiotic utilization, microbial colonization patterns, and nutrient absorption capacity along the intestine (Awad et al. 2009; Adhikari et al. 2017).

Claudins are important components of tight junctions, which control the passage of chemicals and ions across the epithelial cell layer. The upregulation of claudin in the CELL and MB groups suggested that these additives might enhance the integrity of tight junctions thus improving intestinal barrier function (Awad et al. 2017). Enzymatic hydrolysis of the YCW results in a partially hydrolyzed YCW that is rich in β-glucans and MOS with reduced levels of chitin which can boost the effectiveness of YCW as a prebiotic (Pourabedin and Zhao 2015). On the other hand, downregulation of claudin expression in W group could potentially indicate a negative impact on intestinal barrier function which could be attributed to the presence of chitin in YCW (Yin et al. 2018). Interleukin 1β is a pro-inflammatory cytokine that is important in the mediating of inflammatory reactions (Al-Sadi et al. 2009). The increased expression of IL-1β in the CELL group shows that yeast cell wall components, particularly when enzymatically processed, may be eliciting immune-stimulatory effects. This has the potential to improve the immune response to pathogenic threats in the cecal tonsils. The downregulation of IL-1β expression in the MB and WP groups, on the other hand, suggests that the combination of pure MOS and β-glucan may have anti-inflammatory characteristics, dampening IL-1β production. The W group's additional downregulation of IL-1β expression could be attributed to the unique composition of autolyzed whole yeast cell (Pourabedin and Zhao 2015), which may not have a strong immune-stimulatory effect. Interleukin 10, a cytokine known for its anti-inflammatory properties, plays a crucial role in regulating immune responses and maintaining gut homeostasis (Steen et al. 2020). The increased expression of IL-10 in all supplemented groups (CELL, MB, WP, and W) suggests an increase in anti-inflammatory activity in the gut.

Salmonella challenged birds fed control diet showed numerically lower growth performance although the reduction of performance was not significant. This was anticipated and agreed with previous studies (Abudabos et al. 2017; Teng et al. 2020). The decreased growth performance observed in the challenged birds is likely a result of the damage to the intestinal mucosa caused by the *Salmonella* infection. In contrast, a study conducted by Mountzouris et al. (2009) found that broilers infected with *Salmonella* showed no significant difference in growth compared to healthy birds. These conflicting findings could be attributed to variations in the type of *Salmonella* used, the specific strains or dosage administered, which may have resulted in different levels of stability in the intestinal environment (Malago et al. 2003). Although the supplementation did not induce any discernible alterations in bursa of Fabricius weight among the healthy birds, this suggests that the supplementation with autolyzed whole yeast cell at the higher dosage (W) may positively influence the development of the bursa of Fabricius and consequently enhance immunity during *Salmonella* challenge. The discernible implication from these findings is that dietary supplementation has yielded diverse outcomes concerning both organ weights and relative organ weights. These variations could plausibly be ascribed to the distinctive components and characteristics of the supplements, in conjunction with potential interactions stemming from the presence of *Salmonella* infection.

Previous research found that *Salmonella* challenge has a deleterious impact on intestinal morphology. *Salmonella* inhibited the development of the small intestine by reducing VH and surface area, resulting in a lower intestinal absorptive ability and, finally, a loss in growth performance observed in broiler chickens (Abudabos et al. 2019; Pascual et al. 2020). Interestingly, different treatments had clear effects on the morphometric parameters of the jejunal and ileal villi in broilers. The specific treatments influenced the VH, CD, and their ratios, which are important indicators of morphological integrity, intestinal health, and nutrient absorption capacity (Alkhulaifi et al. 2022). Furthermore, the effects of supplementation varied depending on the concentration and duration of administration. The observed increase in VH in the jujenum of birds in the CELL and MB groups, along with the elevated VH: CD ratio in the MB group, and a decrease in CD in the other groups, indicates a potential restoration of intestinal health and enhanced nutrient absorption capacity, despite the birds challenging with *Salmonella* by day 21(Duarte et al. 2020). This restorative effect may be attributed to the exceptional composition of the CELL and MB group, (MOS and β-glucan). In contrast, on day 35, an unexpected observation was made wherein the VH: CD was adversely influenced across all supplemented groups. The VH: CD ratio is regarded as a better indicator of intestinal absorptive capacity than VH and CD. (Duarte et al. 2020). This observation diverges from the findings of previous studies (Alkhulaifi et al. 2022) and introduces a unique perspective on the effects of supplementation on villous morphology.

The effects of treatments were less consistent at day 35, with some fluctuations in VH and CD values across treatments and segments of the small intestine.

The YCW exerts an immunemodulatory properties attributed to its constituent elements, which exhibit the capacity to engage with receptors located not only along the mucosal linings of animal digestive tracts (Mansour et al. 2002), but also on the surfaces of deleterious bacterial entities (Wellens et al. 2008). In the current study, the data suggests that the different treatment groups exhibit varying responses to the infection in terms of barrier-related genes and immune cytokines which might be due to differences in concentration or composition of the additives. Claudin expression showed varying degrees of upregulation across the treatment groups, indicating different levels of impact on tight junction integrity. Notably, the CELL and MB groups exhibited upregulation, suggesting reinforced tight junctions in response to infection. Similarly, occludin expression also varied among treatment groups, with the W group showing a minor upregulation and the CELL, WP, and MB groups displaying substantial increases. This suggests a range of responses, from mild impact to strong reinforcement of tight junctions, likely as a protective mechanism against *Salmonella* infection.

Unlike healthy birds, IL-1β expression was upregulated in all supplemented groups with different levels indicating immune response activation. Although WP and MB groups showed downregulation of IL-1β expression in healthy birds, one of the important results that IL-1β expression increased in these groups (1.97-fold and 2.28-fold, respectively) indicating a consistent but slightly less intense immune response to *Salmonella* infection. Like IL-1β, the IL-10 expression differs in *Salmonella* infected birds. In healthy birds, all supplementation exerts an anti-inflammatory effect appear as upregulation in IL-10 expression. However, after the *Salmonella* challenge, IL-10 expression was downregulated in WP and MB groups, this could signify a more complex regulatory pattern, possibly involving other immune factors.

To further elucidate the mechanisms underlying the observed effects, it is crucial to consider the intricate interplay between the supplemented yeast cell wall components, the gut microbiota, and the host immune system. The enhanced growth performance and improved intestinal morphology seen with enzymatically treated YCW (CELL) may be attributed to its capacity to selectively modulate the gut microbiota, favoring the proliferation of beneficial bacteria known to enhance nutrient absorption and gut health (Yang et al. 2008; Aruwa et al. 2021). This shift in microbial populations can subsequently influence the host immune system through the production of microbial metabolites and the direct interaction of bacterial components with intestinal epithelial cells and immune cells. Furthermore, the differential expression of pro-inflammatory (IL-1β) and anti-inflammatory (IL-10) cytokines across the treatment groups highlights the immunomodulatory potential of the various YCW fractions. The binding of specific components like β-glucans to pattern recognition receptors on immune cells (Mansour et al. 2002) can trigger downstream signaling pathways, influencing cytokine production and ultimately impacting intestinal barrier integrity, as evidenced by the varying expression of claudins and occludins. Therefore, the observed outcomes are likely a result of a complex synergy between the direct effects of YCW components on the host, their influence on the gut microbio.

Conclusion

Our findings contribute to the growing body of literature on YCW supplementation in broilers, highlighting the differential effects of various YCW preparations on growth performance, intestinal morphology, barrier function, and immune responses, particularly in the context of a *Salmonella Typhimurium* challenge. The study underscores the potential benefits of enzymatically treated YCW in improving growth and mitigating the adverse effects of *Salmonella* infection, while also revealing complex and sometimes contrasting effects of different YCW components on intestinal morphology and immune modulation, necessitating further research to optimize their application in poultry production.

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Author contributions The authors' contributions covered many elements of the study. Ozge Sizmaz oversaw conceptualizing, visualizing, experimental design and drafting the original manuscript. Pınar Sacakli oversaw experimental design and sampling. Elsayed Mickdam was responsible for formal analysis, data collecting, and revised the initial manuscript. Alev Gurol Bayraktaroglu and Burcu Ekim were responsible for methodology, investigation, and project administration. All authors provide feedback on previous versions of the text, evaluated the final draft, and authorized it for submission.

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Data availability No datasets were generated or analysed during the current study.

Declarations

Competing interests The authors declare no competing interests.

Ethics approval This trial was approved by the Animal Experiments Local Ethical Committee of the University of Ankara (201817110).

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