# Differences in Gel Properties of Soy Protein Induced by Fermentation with Different Lactic Acid Bacteria and Comparative Analysis of Related Genomes

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**Abstract.** Lactic acid bacteria (LAB) play a crucial role in the formation and functional property regulation of soy protein gels. However, significant differences exist in the effects of different strains on gel properties, and the underlying molecular-level differences have not been fully elucidated. In this study, eight LAB strains commonly used in food production, including Lactobacillus acidophilus, Lactobacillus plantarum, Lacticaseibacillus casei, Lacticaseibacillus paracasei, Lacticaseibacillus rhamnosus, Leuconostoc mesenteroides, Lactococcus lactis, and Streptococcus thermophilus, were selected to systematically evaluate five core texture indicators of fermented soy protein gels: hardness, springiness, cohesiveness, gumminess, and chewiness. Meanwhile, combined with the genome sequencing data of each strain, the differences in the effects of different strains on gel texture were compared, and functional enrichment analysis was performed on differentially expressed coding genes. The results showed that the eight LAB strains exhibited differences in the number of coding genes and unique genes in carbohydrate-related pathways, nucleotide metabolism pathways, lysine/arginine biosynthesis pathways, and ABC transporter pathways, and the induced gels also showed different texture properties. This study not only reveals the significant differences in texture properties of soy protein gels induced by different LAB strains but also further clarifies the core root factor regulating gel properties, namely the differences in strain coding genes. The purpose of this study is to provide a theoretical reference and key research entry point for the subsequent directional improvement of soy protein gel properties through precise regulation of strain genes.

**Keywords:** Lactic acid bacteria; Soy protein gel properties; Genome comparison; Gene enrichment analysis.

## 1. Introduction

In today's society, a variety of plant-based products can be developed based on soy protein gels, and plant-based foods are widely recognized as one of the development trends of future foods. Soy Protein Isolate (SPI) is a high-purity plant protein product obtained through processing, which has extremely high nutritional value and is widely used as a raw material in food processing [1]. Its gel, as the core form of SPI functionalization, forms a three-dimensional network structure relying on intermolecular hydrogen bonds, disulfide bonds, hydrophobic interactions, etc. [2]. Due to its gel texture properties, soy protein gel provides the possibility for the food industry to develop various products. Although soy protein gel properties have broad development potential, their texture properties still have shortcomings in application. It is hoped that the formation of soy protein gels induced by LAB can improve their characteristic indexes [3] to better meet the processing needs of different products.

Lactic acid bacteria (LAB) are a group of Gram-positive bacteria that can ferment carbohydrates to produce a large amount of lactic acid and are widely present in fermented foods (such as yogurt, kimchi, natto) and the human intestinal tract [4]. The eight LAB strains in this paper are all food-grade and have significant differences in metabolic characteristics. Lactobacillus acidophilus, Lactobacillus plantarum, Lacticaseibacillus casei, Lacticaseibacillus paracasei, and Lacticaseibacillus rhamnosus all belong to the genus Lactobacillus, which are Gram-positive bacilli, facultative anaerobic, produce L-lactic acid through homofermentation, have intestinal colonization ability, and are widely used in dairy processing [5]. Among them, Lactobacillus acidophilus can secrete antibacterial substances to inhibit pathogenic bacteria [6]; Lactobacillus plantarum has a broad carbon

source utilization spectrum, can be used to ferment fruits and vegetables to shorten the cycle, and can also generate antioxidant substances [7,8]; Lacticaseibacillus casei has strong stress resistance and protease activity, which can promote protein hydrolysis; Lacticaseibacillus paracasei has high protease activity, which can improve the palatability of fermented milk, and its polysaccharides can enhance the intestinal barrier [9]; Lacticaseibacillus rhamnosus has outstanding adhesion ability [10]; Streptococcus thermophilus often ferments synergistically with Lactobacillus bulgaricus, forming a symbiotic metabolic relationship, and Streptococcus thermophilus produces EPS, which improves the viscosity of yogurt by combining with milk protein. Meanwhile, Leuconostoc mesenteroides belong to the genus Leuconostoc, and Lactococcus lactis belongs to the genus Lactococcus. The former produces $CO_2$ and dextran through heterofermentation [11], which is a key strain for flavor formation and texture improvement of kimchi and cheese [7]; the latter can generate flavor substances such as n-hexanal and ethyl acetate through amino acid metabolism and is mostly used for flavor regulation of cheese and fermented milk. At present, research on the mechanism of soy protein gel formation induced by LAB is still limited, especially in exploring the genetic level of differences in gel properties caused by different LAB strains. The specific association between key functional genes and gel formation characteristics has not been clarified.

The purpose of this paper is to reflect the differences of soy protein gels induced by eight LAB strains through five-dimensional numerical indicators through experimental measurement, and to explore the root causes of fermentation-induced differences based on genomic analysis. Through gene enrichment analysis and other comparisons of experimental results, it provides precise research targets for subsequent screening of dominant LAB strains suitable for soy protein gel fermentation, and also provides a scientific basis for optimizing the fermentation process of soy protein gels and improving the quality and stability of related products, helping the technical research of related food industries.

## 2. Materials and Methods

### 2.1. Experimental Materials

Strains (Lactobacillus acidophilus, Lactobacillus plantarum, Lacticaseibacillus casei, Lacticaseibacillus paracasei, Lacticaseibacillus rhamnosus, Leuconostoc mesenteroides, Lactococcus lactis, Streptococcus thermophilus) were obtained from the College of Food Science, Northeast Agricultural University, and cultured in MRS medium at 37°C [12].

Soy Protein Isolate (SPI, 90%) was purchased from Harbin Gaoke Soy Food Co., Ltd (Heilongjiang, China).

### 2.2. Preparation of Fermentation-Induced Gels

The dispersion containing 10% SPI and 2% glucose was stirred at 25°C for 4 hours (350g) using a magnetic stirrer [12]. The stirred SPI dispersion was placed at 4°C for 12 hours and then sterilized at 105°C for 15 minutes. All strains (4%) were inoculated into the SPI dispersion and fermented for 0, 2, 4, 6, 8, and 10 hours [13]. The formation of the gel was evaluated by inverting the sample at room temperature [14,15]. A gel was considered formed if it remained stable and did not fall off after 10 minutes.

### 2.3. Measurement of Induced Gel Property Indicators

The fermentation-induced gels of the eight processed LAB strains were divided into groups fermented for 4, 6, 8, and 10 hours. The hardness, springiness, cohesiveness, gumminess, and chewiness were measured using a texture analyzer (Stable Micro Systems, TA.XT PlusC, UK) as follows:

Hardness: The parameters were adjusted with reference to [12]. A P/0.5S spherical probe was used, and each sample was compressed twice axially with a compression ratio of 45%. The pre-test speed

was set to 5.0 mm/s, the test speed was 2.0 mm/s, and the post-test return speed was also 2.0 mm/s. The test interval was 8 seconds, and the total test duration was 30 seconds.

Springiness and Cohesiveness: Springiness and cohesiveness were measured using a texture analyzer (Stable Micro Systems, TA. XT PlusC, UK) with Texture Profile Analysis (TPA) [16]. Four parallel experiments were conducted to observe and analyze data differences.

Gumminess and Chewiness: As derived parameters, gumminess and chewiness were calculated based on data measured by combining the texture analyzer and TPA method using core TPA parameters.

### 2.4. Statistical Analysis of Data

The mean and standard deviation of each characteristic at different time points were calculated through the Omicshare website (https://www.omicshare.com/tools/), and one-way analysis of variance (One-way ANOVA) was performed to test the main effects of bacterial species and treatment time on the characteristics. When $P<0.05$, Duncan's multiple comparison method was used for inter-group difference testing; letters (a, b, c, etc.) were used for significant difference grouping, where the same letter indicates no significant difference between groups, and different letters indicate significant difference ($P<0.05$). Meanwhile, the characteristic differences of different bacterial species and the temporal dynamic characteristic differences of the same bacterial species were analyzed to ensure the statistical reliability of the results.

### 2.5. Collection of Genomic Data

Genetic information on Lactobacillus acidophilus (GCF_034298135.1), Lactobacillus plantarum (GCF_009913655.1), Lacticaseibacillus casei (GCF_000829055.1), Lacticaseibacillus paracasei (GCF_000155515.2), Lacticaseibacillus rhamnosus (GCF_006151905.1), Leuconostoc mesenteroides (GCF_000014445.1), Lactococcus lactis (GCF_003176835.1), and Streptococcus thermophilus (GCF_903886475.1) was downloaded from the NCBI database.

### 2.6. Genomic Enrichment Analysis

The coding genes of the corresponding bacterial species were obtained through Eggnog online annotation, and further KEGG and GO functional enrichment analyses were performed on the Omicshare platform (https://www.omicshare.com/) to obtain the significantly enriched functional pathways and functional terms in each strain. The number of coding genes and unique genes in the functional pathways of the bacterial species were searched and compared to analyze the root causes of fermentation-induced differences.

## 3. Results and Discussion

The properties of gels induced by different strains at different times were measured using a texture analyzer,as shown in Figure 1. In the experiment, the gel induced by Lacticaseibacillus casei formed the fastest, initially appearing at 2 hours, while gels induced by other strains gradually formed at 4 hours. Therefore, 4 hours was uniformly used as the starting point for measurement.

### 3.1. Analysis of Differences in Properties of Eight Induced Gels

#### 3.1.1. Hardness Differences

Hardness is one of the essential properties of soy protein gels and has important analytical value. Higher hardness indicates a more compact three-dimensional network structure and higher stability of the generated gel, as shown in the hardness relationship reported in the literature [12]. In the experiment, the hardness of gels induced by eight bacterial species was measured at different times (4, 6, 8, and 10 hours). At 8 hours when the gel was relatively stable, the values ranged from 180.05±9.49 to 256.64±16.83, indicating significant differences in the catalytic effects of the strains

[12]. Through further multiple comparison analysis, as shown in Figure 1, the strains can be roughly divided into Groups I-IV according to their growth trends:

Group I: Although significantly higher than other strains at 2 and 4 hours, the fermentation effect was slow afterward, including Lacticaseibacillus casei and Streptococcus thermophilus;

Group II: The gels induced by these strains had significantly lower hardness than other gels during fermentation, including Lactobacillus plantarum and Lacticaseibacillus rhamnosus;

Group III: Showing a stable growth trend with the extension of fermentation time, including Lacticaseibacillus paracasei, Leuconostoc mesenteroides, and Lactococcus lactis;

Group IV: The hardness of the gel induced by Lactobacillus acidophilus showed an increasing trend, but the growth rate was unstable.

Notably, Lacticaseibacillus casei in Group I had the relatively fastest fermentation rate in the early stage. The gel induced by this strain formed the fastest, with a hardness of 147.18±15.25 at 4 hours, which was significantly higher than other gels ($P<0.05$). However, the growth rate decreased significantly from 6 to 10 hours, being overtaken by other gels. At the other extreme, Group II (Lactobacillus plantarum and Lacticaseibacillus rhamnosus induced gel groups) had lower hardness than other gels during fermentation. When the gel was stable at 10 hours, their hardness values were 180.04±9.49 and 180.63±15.24, respectively, which were significantly lower than other gels ($P<0.05$). Meanwhile, the gels induced by Lacticaseibacillus paracasei, Leuconostoc mesenteroides, and Lactococcus lactis in Group III showed a steady growth trend, increasing from low hardness at 4 hours to the high hardness echelon at 10 hours, which was significantly higher than other gels ($P<0.05$). In summary, based on the needs of efficient food industrial production, attempts can be made to use strains similar to Lacticaseibacillus casei for gel induction to improve production efficiency [12].

### 3.1.2. Springiness Differences

Springiness, i.e., "taste", has an important impact on the sensory properties of foods produced with soy protein gels. The springiness of soy protein gels fermented and induced by eight LAB strains was measured by TPA. The data fluctuation tended to be stable after 8 hours, and the overall data ranged from 0.65 to 0.87 between 8 and 10 hours. According to the differences in springiness growth of the eight gels, they can be roughly divided into Groups I-IV:

Group I: The springiness of the gel induced by these strains first increased and then decreased, including Lactobacillus acidophilus;

Group II: The gels induced by Lacticaseibacillus casei and Lacticaseibacillus paracasei formed quickly in the early stage with high springiness, but gradually weakened to a medium level in the later stage;

Group III: The springiness of the gel induced by these strains was consistently lower than that of other gels during fermentation, including Lactobacillus plantarum and Lacticaseibacillus rhamnosus;

Group IV: The springiness of the gel induced by these strains was relatively high overall in the stable period (8-10 hours), ranking in the second echelon of springiness, with no significant difference within the group, including Leuconostoc mesenteroides, Lactococcus lactis, and Streptococcus thermophilus.

The study showed that the springiness of the gel induced by Lactobacillus acidophilus in Group I continued to increase, from the lowest 0.73±0.06 at 4 hours to the highest 0.87±0.16 at 10 hours, which was significantly ahead of other gels ($P<0.05$). For Lacticaseibacillus casei and Lacticaseibacillus paracasei in Group II, although there were abnormal fluctuations at individual time points, the springiness of the induced gels generally showed a trend of first high and then low from 4 to 10 hours, decreasing from the highest 0.88±0.08 and 0.93±0.03 to the lowest 0.75±0.04 and 0.73±0.03, respectively. In Group IV, Leuconostoc mesenteroides was significantly higher than the other two gels at 4 hours ($P<0.05$). At 6 hours, with the increase in springiness of Lactococcus lactis and Streptococcus thermophilus, the difference in springiness among the three gels narrowed. When the gel was stable between 8 and 10 hours, there was no significant difference in springiness among the three induced gels. Overall, through appropriate time regulation, gels with high springiness

characteristics can be efficiently obtained by induction with Lacticaseibacillus casei or Lacticaseibacillus paracasei, which is convenient for subsequent food processing and application.

### 3.1.3. Cohesiveness Differences

Cohesiveness reflects the continuity and strength of the three-dimensional network structure of the gel, and this property is directly related to the texture quality and sensory acceptability of the product. The experiment showed that the gel was stable at about 8 hours, and the cohesiveness ranged from 0.42±0.00 to 0.51±0.01. Therefore, the eight induced gels were divided into Groups I-IV according to significance and growth trends:

Group I: The gel induced by Lactobacillus acidophilus showed an increasing trend, gradually becoming part of the first echelon with high cohesiveness as fermentation time extended;

Group II: Maintaining low cohesiveness and lagging behind the other 7 gels throughout fermentation, with values ranging from 0.42±0.00 to 0.44±0.02 between 8 and 10 hours, including Lactobacillus plantarum and Lacticaseibacillus rhamnosus groups;

Group III: The gels induced by these strains had high cohesiveness, fluctuating around 0.50 but with poor stability, including Lacticaseibacillus casei and Lacticaseibacillus paracasei;

Group IV: Maintaining high cohesiveness values for a long time with good stability, including Leuconostoc mesenteroides, Lactococcus lactis, and Streptococcus thermophilus groups.

The experiment found that except for an abnormal low value of 0.45±0.02 at 6 hours, the gel induced by Lactobacillus acidophilus in Group I generally showed an increasing trend, from 0.48±0.03 at 4 hours to 0.50±0.02 at 10 hours, moving from lagging behind other gels to being part of the high-cohesiveness gel echelon. For the gels induced by Lacticaseibacillus casei and Lacticaseibacillus paracasei in Group III, the cohesiveness fluctuated during fermentation. Starting from high cohesiveness at 4 hours, it slightly increased to 0.51±0.01 (for Lacticaseibacillus casei) and slightly decreased to 0.48±0.01 (for Lacticaseibacillus paracasei) at 8 hours, then both reached the same cohesiveness value of 0.48±0.01 at 10 hours, showing poor overall stability. In contrast, the gels induced by Group IV had the characteristics of high cohesiveness values and good stability. During 4-10 hours, the gels induced by the three strains consistently showed high cohesiveness with no significant difference within the group. At 8 hours when the gel was stable, the cohesiveness values were 0.49±0.01, 0.49±0.01, and 0.48±0.02, respectively. Good cohesiveness ensures the stability of the gel's shape during processing. Under the dual demands of high quality and high efficiency, Lacticaseibacillus casei, Lacticaseibacillus paracasei, Leuconostoc mesenteroides, Lactococcus lactis, and Streptococcus thermophilus are all good choices for gel-inducing strains.

### 3.1.4. Gumminess and Chewiness Differences

In TPA analysis, gumminess is closely related to hardness and cohesiveness, and as a parameter describing the sensory properties of food, it represents the part related to the "viscous" feeling. Chewiness, i.e., "chewiness", refers to the work required to chew a solid sample to a swallowable state. Its value is closely related to hardness, cohesiveness, and springiness. As shown in Figure 1, the numerical results of gumminess and chewiness of the above eight gels were proportionally similar. With the extension of fermentation induction time, the values of the eight induced gels all showed an upward trend. According to the growth rate characteristics, they can be divided into Groups I-IV:

Group I: Rapid gel formation, with significantly higher two properties than other gels in the early stage but insufficient sustainability, showing a lagging trend in the later stage, including Lacticaseibacillus casei and Streptococcus thermophilus;

Group II: After 4 hours, gumminess and chewiness were significantly lower than other gels, including Lactobacillus plantarum and Lacticaseibacillus rhamnosus;

Group III: With the extension of fermentation time, the characteristic indexes increased significantly, ranking in the first echelon of high properties when the gel was stable (8-10 hours), including Lacticaseibacillus paracasei, Leuconostoc mesenteroides, and Lactococcus lactis;

Group IV: The overall changes of the gel induced by Lactobacillus acidophilus were similar to those of Group III, but the overall growth rate was slightly lower, resulting in slightly lower values of the two properties than Group III.

The study found that at 4 hours, the two characteristic values of the gel induced by Lacticaseibacillus casei in Group I were significantly higher than other gels ($P<0.05$), and the gel induced by Streptococcus thermophilus was similar, with values second only to Lacticaseibacillus casei at 4 hours. The growth rate of the above two strains decreased significantly from 6 to 10 hours, lagging behind other gels, but still higher than those of the gels induced by Lactobacillus plantarum and Lacticaseibacillus rhamnosus. In addition, the characteristic values of the gels induced by Group III increased rapidly with time. The gumminess and chewiness levels at 8-10 hours were higher than other gels, showing high gumminess at 10 hours. Overall, both gumminess and chewiness are derived parameters calculated from hardness, springiness, etc., using similar formulas [16], so the results are proportionally similar, but these results can still effectively reflect the texture stability of the gel. The experiment showed that the induction conditions of Lacticaseibacillus paracasei can not only meet the demand for high efficiency but also the demand for the stability of the gel structure, which is conducive to subsequent processing.

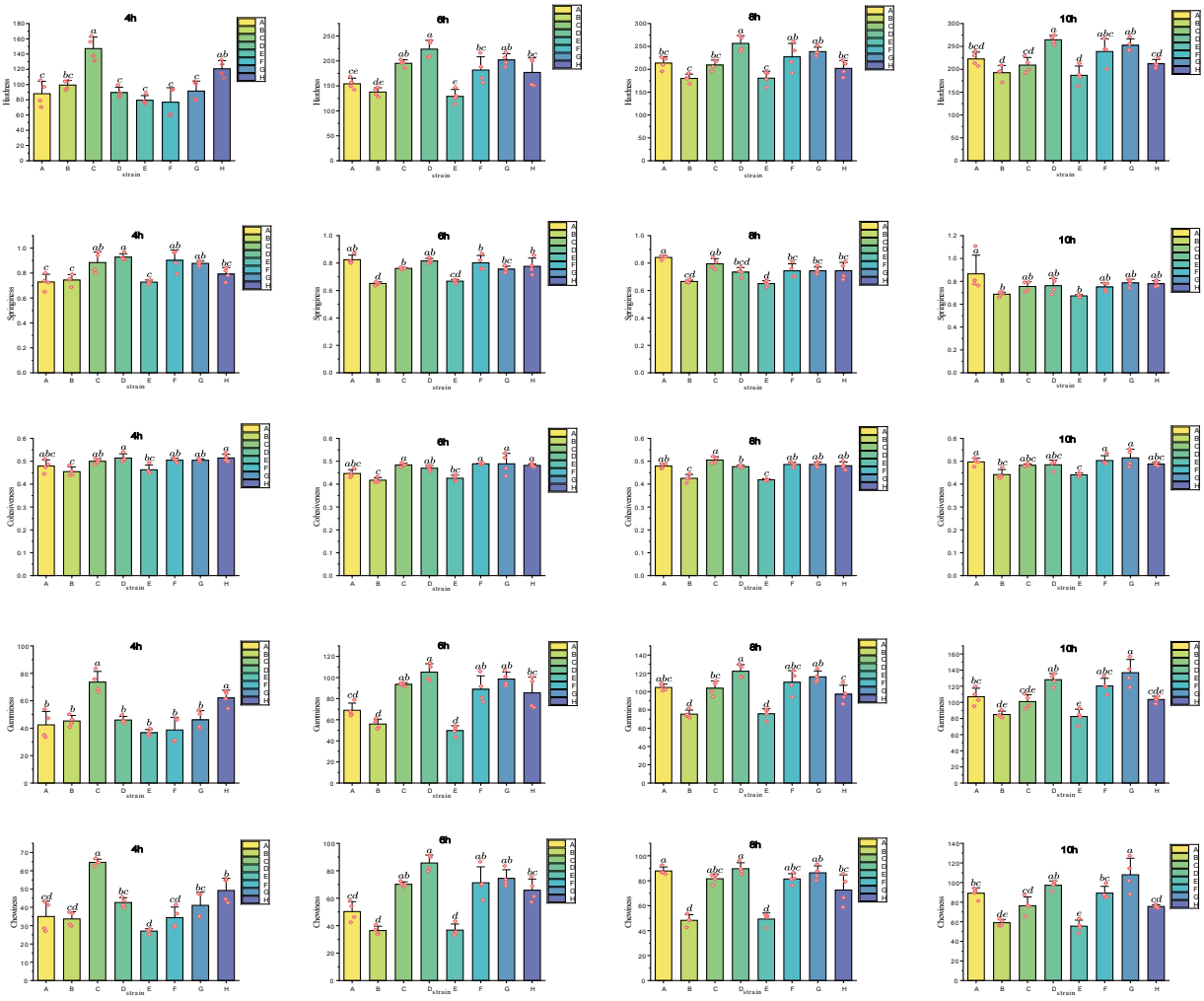


**Figure 1.** Comparison of characteristic measurement results at different time points during the gelatinization process induced by lactic acid bacteria. Specifically: Lactobacillus acidophilus (A), Lactobacillus plantarum (B), Lactobacillus casei (C), Lactobacillus paracasei (D), Lactobacillus rhamnosus (E), Leuconostoc mesenteroides (F), Lactococcus lactis (G), Streptococcus thermophilus (H). Different letters (a-d) indicate significant differences ($P < 0.05$).

### 3.1.5. Discussion on Differences in Induced Gel Properties

The five properties of the induced gel—hardness, springiness, cohesiveness, gumminess, and chewiness—collectively reflect the texture of the formed gel and have important reference significance for subsequent processing [17]. The texture properties of the induced gel are inseparable from the influence of factors such as the properties of the soy protein matrix [18,19], the metabolic characteristics of the strain [17,20], environmental regulatory factors [21], and exogenous synergistic substances [22]. The experiment found that the three groups of strains with better induction effects had the following reasons. Firstly, Lacticaseibacillus casei and Streptococcus thermophilus belong to the first echelon with rapid gel formation, among which Lacticaseibacillus casei showed this characteristic more obviously. The former achieves rapid gel formation by secreting exopolysaccharides (EPS) to fill the gaps in the protein network, releasing proteases to hydrolyze soy protein into short peptides to promote cross-linking, and moderately producing acid to accelerate aggregation[13,23]. The latter can rapidly form gels through the ability of protease PrtS to hydrolyze soy protein into small molecule peptides to promote cross-linking, rapid acid production, and EPS secretion [24], but the subsequent continuous growth of properties is lacking. Secondly, Lacticaseibacillus paracasei, which has outstanding properties in the middle stage, mainly benefits from the synergistic effect of protease hydrolysis and acid production. In the middle stage, it optimizes the texture by hydrolyzing 7S and 11S globulins [25], regulating pH, and synergistically filling the network with EPS [26]. Meanwhile, studies have shown that Lactococcus lactis and Leuconostoc mesenteroides, which have advantages in later properties, can optimize the texture conditions of soy protein gels through metabolic acid production and peptidase hydrolysis of proteins (for Lactococcus lactis) and constructing a "protein-polysaccharide" network (for Leuconostoc mesenteroides) [27]. In summary, the three groups of strains can be selected according to different needs to form target-induced strains, and the direction of studying LAB-induced protein gels is refined [28] to better develop plant-based foods.

### 3.2. Comparative Analysis of LAB Genomic Differences

In this study, the whole-genome data of 8 LAB strains were downloaded from the NCBI database, including Lactobacillus acidophilus, Lactobacillus plantarum, Lacticaseibacillus casei, Lacticaseibacillus paracasei, Lacticaseibacillus rhamnosus, Leuconostoc mesenteroides, Lactococcus lactis, and Streptococcus thermophilus. After annotating the above genomic data using the EggNOG online functional annotation tool, the number of coding genes for each strain was obtained as follows: 1773, 2839, 2607, 2652, 2538, 1940, 2137, and 1549. Statistical results showed that among the 8 strains, Streptococcus thermophilus had the least number of coding genes (1549), while Lactobacillus plantarum had the most (2839). It is speculated that the difference in the number of coding genes may enable Lactobacillus plantarum to have richer functional diversity and broader biological characteristics.

### 3.3. Analysis of Gene Function Differences

We further explored the functional differences of strains through KEGG and GO functional enrichment analyses. Through these two types of functional enrichment analyses, we can not only obtain the significantly enriched functional pathways and functional terms in each strain but also combine the key physiological indicators of the soy protein gel fermentation process to deeply explain the molecular mechanisms underlying the differences in fermentation efficiency, fermentation product texture, etc., of the eight LAB strains in soy protein gel fermentation.

### 3.4. KEGG Enrichment Analysis of Strain Functional Differences

The results of the KEGG enrichment analysis, as shown in Table 1 and Figure 2, revealed that 603, 952, 779, 902, 875, 734, 771 616 genes in Lactobacillus acidophilus, L. plantarum, Lacticaseibacillus casei, L. paracasei, L. rhamnosus, Leuconostoc mesenteroides, Lactococcus lactis, and Streptococcus thermophilus were implicated in 1 Some of these pathways are essential in case of soy protein gel

fermentation. The metabolism of carbohydrates (ko00010, ko00500, ko01200, et cetera) provides energy and intermediates that have a textural effect on the gel and flavor. Metabolite nucleotide (ko00230, ko00240) and lysine/arginine biosynthesis (ko00300, ko00220) facilitate bacterial growth and provide the extracellular proteases with substrates, which promotes soy protein hydrolysis and cross-linking. The formation of gels is further mediated by the ABC transporter pathway (ko02010) that facilitates the secretion of proteins, transport of EPS precursors and nutrient intake. All these pathways together guarantee good fermentation and formation of gels.

**Table 1.** Statistical Number of Genes Annotated in KEGG Pathways of Eight LAB Strains.

| KEGG pathway | *L.acidophilus* | *L.plantarum* | *L.casei* | *L.paracasei* | *L.rhamnosus* | *L.mesenteroides* | *L.lactis* | *S.thermophilus* |
|---|---|---|---|---|---|---|---|---|
| Purine metabolism | 41 | 52 | 44 | 45 | 47 | 46 | 42 | 37 |
| Pyrimidine metabolism | 27 | 32 | 32 | 32 | 34 | 29 | 31 | 29 |
| Biosynthesis of amino acids | 50 | 104 | 80 | 96 | 86 | 104 | 111 | 91 |
| Biosynthesis of amino acids | 47 | 91 | 57 | 64 | 65 | 80 | 81 | 60 |
| Lysine biosynthesis | 15 | 20 | 17 | 19 | 17 | 19 | 14 | 14 |
| Arginine biosynthesis | 7 | 16 | 8 | 8 | 8 | 14 | 18 | 16 |
| ABC transporters | 50 | 75 | 54 | 92 | 76 | 59 | 62 | 49 |

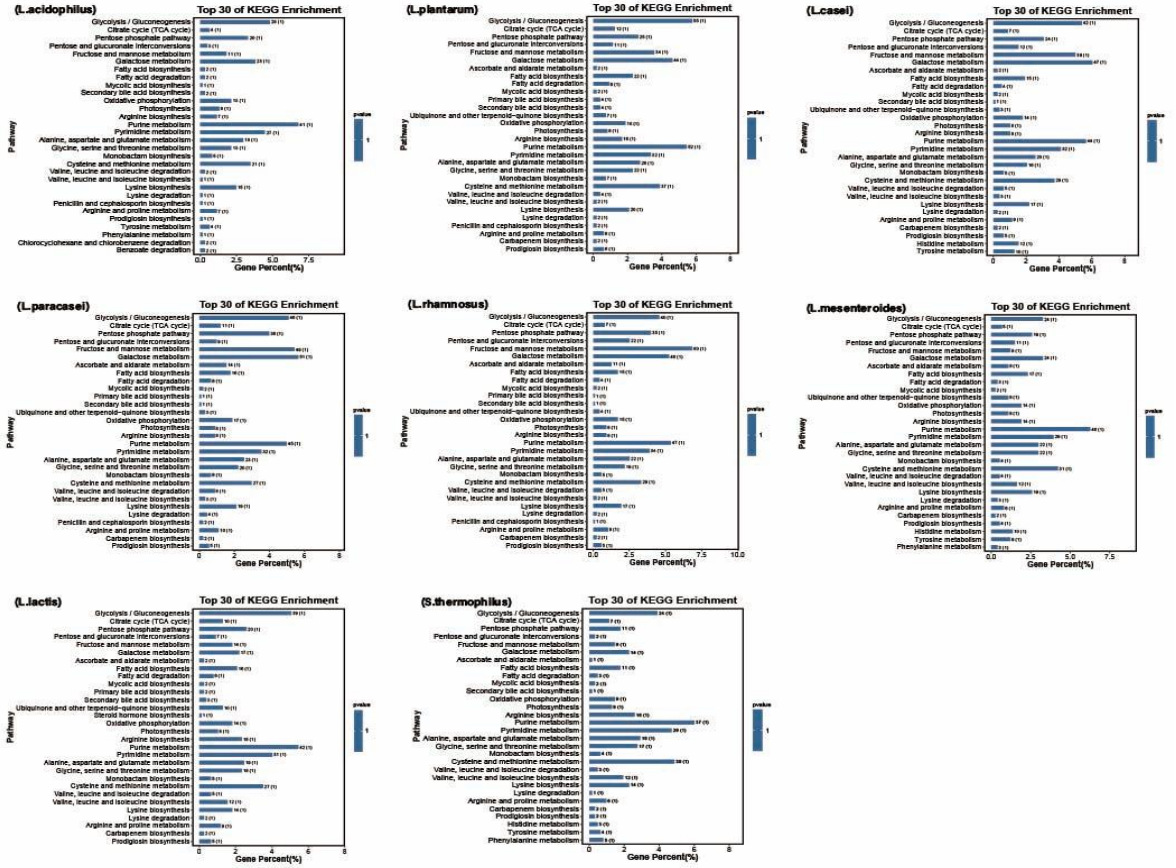


**Figure 2.** Statistical chart of KEGG enrichment analysis results for different lactic acid bacterial strains, showing the number of coding genes in thirty major core pathways for each of the eight strains.

### 3.4.1. Carbohydrate-Related Pathways

Carbohydrate-related pathways include glycolysis, tricarboxylic acid (TCA) cycle, starch and sucrose metabolism pathway, fatty acid biosynthesis pathway, and carbon metabolism pathway. There are certain differences in the coding genes of the eight strains involved in these pathways.

The glycolysis pathway, as shown in Figure 3, is the energy support link for gel formation and property regulation, and is a key pathway for organisms to maintain energy and carbon source homeostasis. Lactobacillus plantarum has the most genes involved in this pathway, while Streptococcus thermophilus and Leuconostoc mesenteroides have the least. In addition, it is worth noting that Lacticaseibacillus casei has a unique coding gene for fructose-bisphosphate aldolase, class I [EC:4.1.2.13], Lactococcus lactis has unique coding genes for acetyl-CoA synthetase [EC:6.2.1.1] and glucose-1-phosphatase [EC:3.1.3.10], and Leuconostoc mesenteroides has unique coding genes for phosphoglycerate kinase [EC:2.7.2.3] and enolase 1/2/3 [EC:4.2.1.11]. These genetic differences may lead to significant differences in glucose utilization efficiency and anaerobic fermentation metabolite production capabilities among different strains.

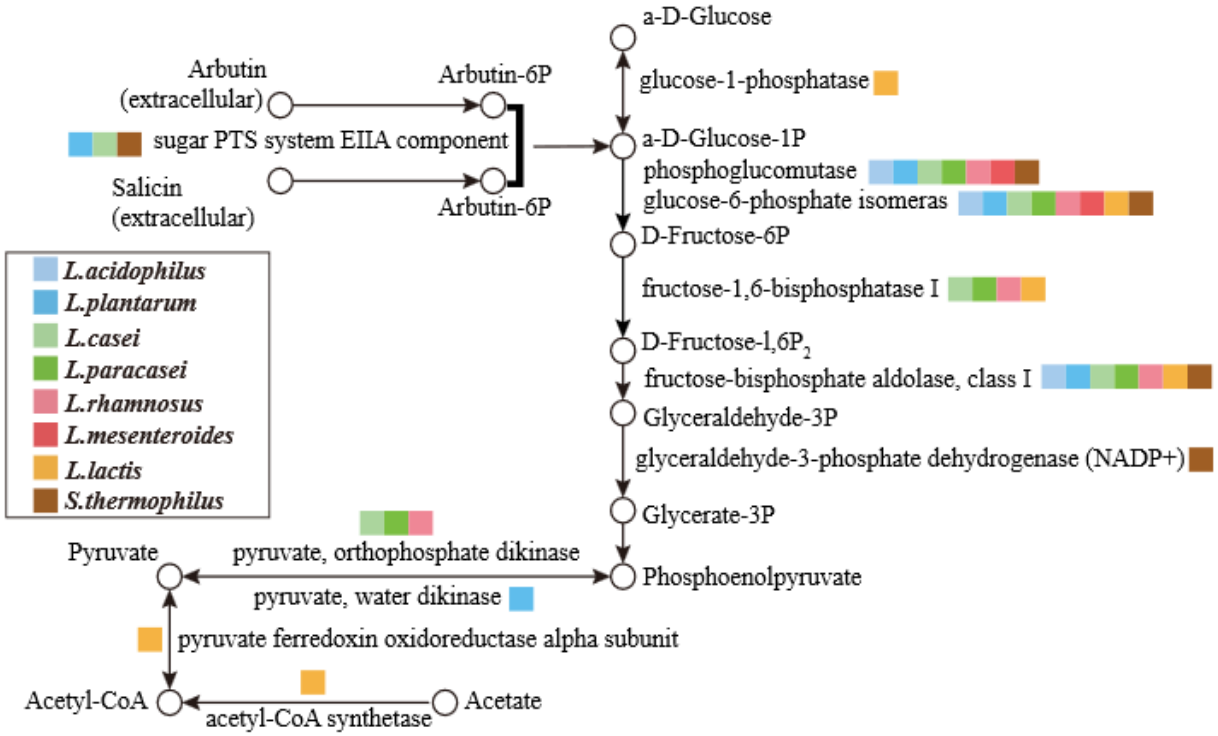


**Figure 3.** The glycolysis.

The TCA cycle, as shown in Figure 4, is not only a key energy metabolic pathway in aerobic respiration but also a junction of carbohydrate, fat, and protein metabolism. It can generate key intermediate products through anaplerotic pathways, contributing to LAB metabolism and gel property regulation. Lactobacillus plantarum has the most genes involved in this pathway, while Lactobacillus acidophilus has the least. Notably, Lactobacillus plantarum has a unique coding gene for fumarate hydratase, class I [EC:4.2.1.2], Lacticaseibacillus paracasei has a unique coding gene for the 2-oxoglutarate dehydrogenase E2 component (dihydrolipoamide succinyltransferase) [EC:2.3.1.61], and Lactococcus lactis has a unique coding gene for pyruvate ferredoxin oxidoreductase alpha subunit [EC:1.2.7.1]. These genetic differences may affect the respiratory efficiency of strains, the synthesis rate of extracellular proteases, the synthesis rate of EPS, etc., thereby influencing gel formation and properties.

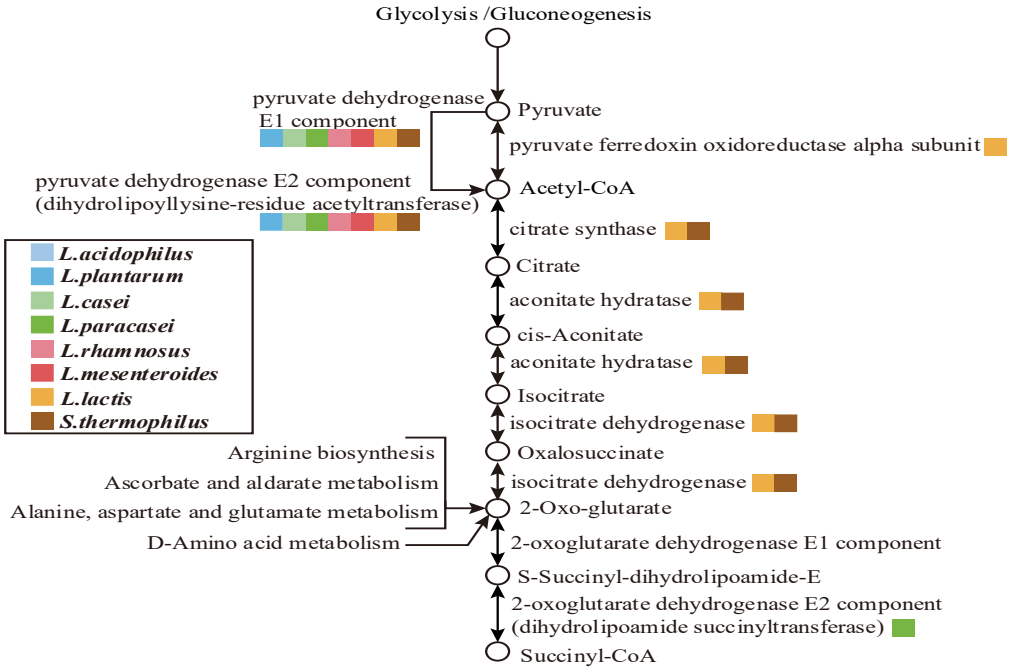


**Figure 4.** The TCA cycle.

The starch and sucrose metabolism pathway, as shown in Figure 5, is not only responsible for the decomposition and synthesis of complex carbohydrates such as starch and sucrose but also can generate EPS precursors, synergistically regulating gel formation efficiency and texture properties. Lactobacillus plantarum has the most genes involved in this pathway, while Streptococcus thermophilus has the least. In addition, it is worth noting that Lactobacillus acidophilus has a unique coding gene for cyclomaltodextrinase/maltogenic alpha-amylase/neopullulanase [EC:3.2.1.54 3.2.1.133 3.2.1.135], Lactobacillus plantarum has unique coding genes for UTP--glucose-1-phosphate uridylyltransferase [EC:2.7.7.9] and alpha,alpha-trehalose phosphorylase [EC:2.4.1.64], Leuconostoc mesenteroides has a unique coding gene for endoglucanase [EC:3.2.1.4], and Streptococcus thermophilus has unique coding genes for 4-alpha-glucanotransferase [EC:2.4.1.25], dextranase [EC:3.2.1.11], and maltose 6'-phosphate phosphatase [EC:3.1.3.90]. These genetic differences may determine the preference of strains for carbon sources such as starch and sucrose, affecting their utilization efficiency of medium carbon sources in soy protein gel fermentation.

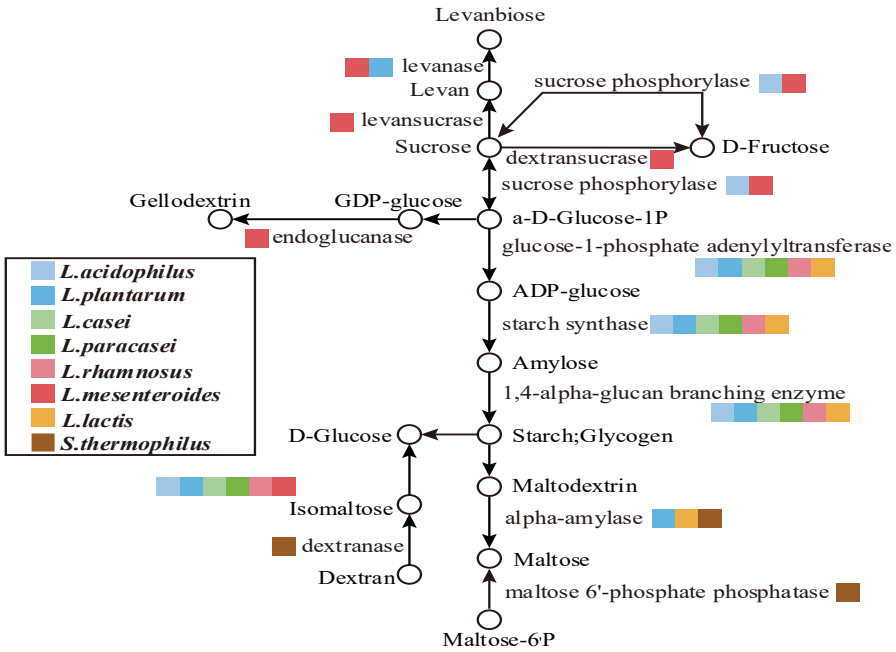


**Figure 5.** The starch and sucrose metabolism.

Fatty acid biosynthesis pathway, as shown in Figure 6, is the main metabolic pathway in which LAB uses carbon source precursors in the synthesis of saturated and unsaturated fatty acids to be used in cell membrane. The highest number of genes in this pathway belongs to Lactobacillus plantarum, whereas the fewest genes in this pathway belong to Lactobacillus acidophilus. Moreover, it is necessary to add that this pathway contains only two Lactobacillus acidophilus coding genes: 3-oxoacyl-[acyl-carrier protein] reductase [EC:1.1.1.100] and medium-chain acyl-[acyl-carrier-protein] hydrolase [EC:3.1.2.21]. Genetic variation can cause variation in the kind, and performance as well as the quantity of fatty acids produced by strains, which in turn influences the fluidity of cell membrane and following metabolism processes.

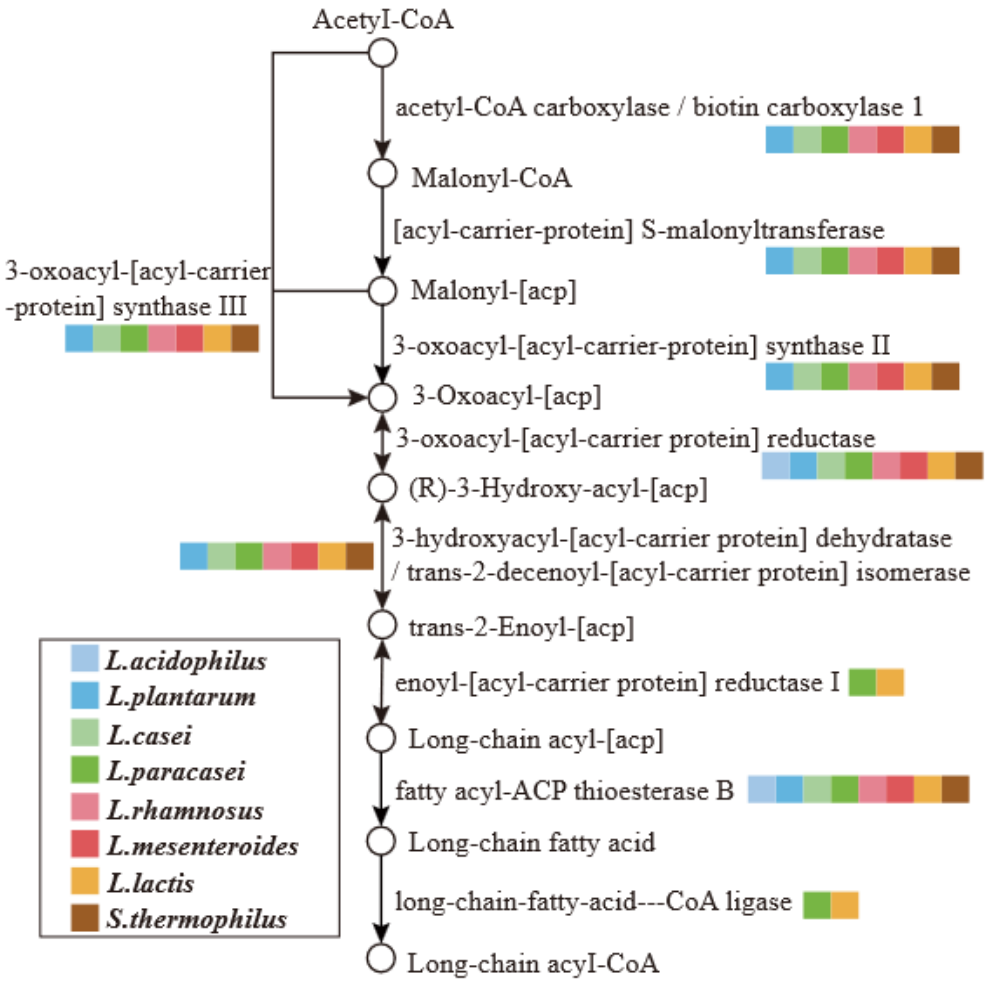


**Figure 6.** The fatty acid biosynthesis.

The carbon metabolism pathway, as shown in Figure 7, is the core pathway integrating the decomposition and transformation of various carbohydrates, directly determining the acid production efficiency and functional molecule synthesis ability of LAB, thereby regulating gel formation rate and texture stability. Lactobacillus plantarum has the most genes involved in this pathway, while Lactobacillus acidophilus has the least. Among them, Lactobacillus plantarum has a unique coding gene for fumarate hydratase, class I [EC:4.2.1.2], Lacticaseibacillus paracasei has a unique coding gene for fructose-bisphosphate aldolase, class I [EC:4.1.2.13], and Leuconostoc mesenteroides has unique coding genes for serine O-acetyltransferase [EC:2.3.1.30] and phosphoglycerate kinase [EC:2.7.2.3]. These genetic differences may enable strains to show different adaptabilities when using different types of carbon sources, affecting their growth and metabolic activity in complex carbon source environments.

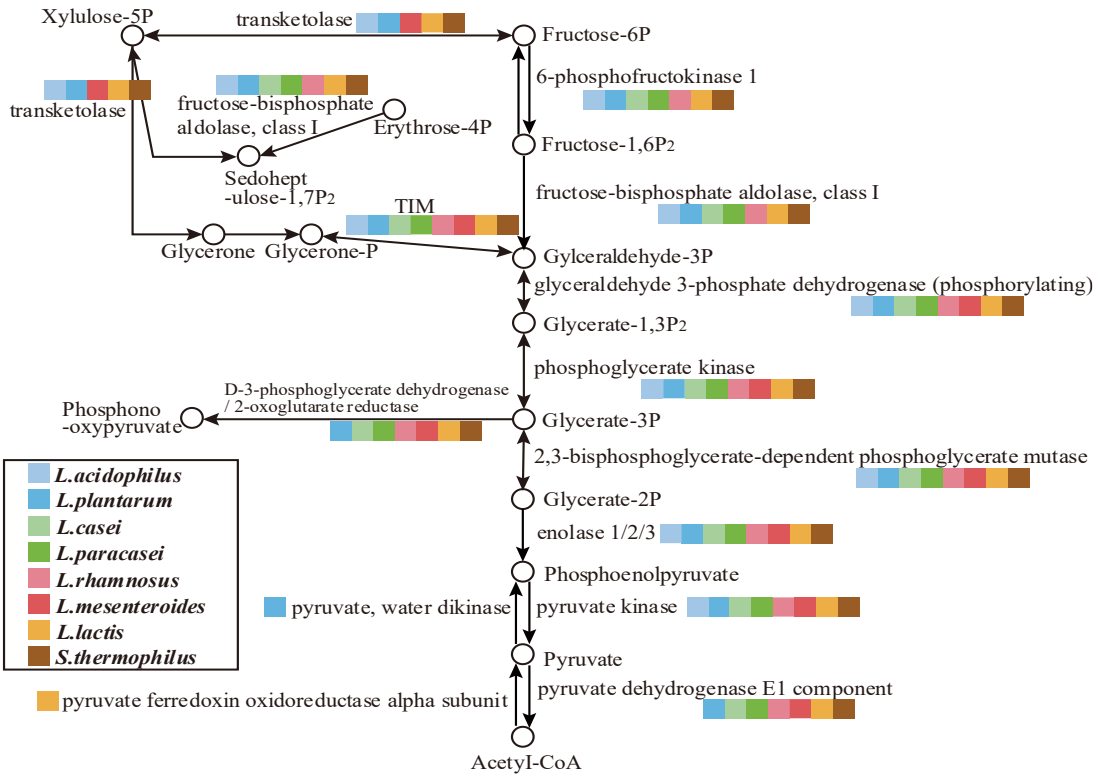


**Figure 7.** The carbon metabolism.

In summary, through the analysis of coding genes of eight LAB strains in five carbohydrate-related pathways (glycolysis, TCA cycle, starch and sucrose metabolism, fatty acid biosynthesis, and carbon metabolism), this study clarified the core difference characteristics of different strains at the functional gene level: in each pathway, there was a significant gap in the number of coding genes between Lactobacillus acidophilus and Lactobacillus plantarum, which were the strains with the least and most genes in the corresponding TCA cycle and fatty acid biosynthesis pathways, respectively; and different strains had pathway-specific unique coding genes. For example, Lacticaseibacillus casei had a unique coding gene for fructose-bisphosphate aldolase, class I [EC:4.1.2.13] in the glycolysis/gluconeogenesis pathway, and Lactobacillus acidophilus had a unique coding gene for cyclomaltodextrinase/maltogenic alpha-amylase/neopullulanase [EC:3.2.1.54 3.2.1.133 3.2.1.135] in the starch and sucrose metabolism pathway. These genetic differences not only led to obvious differentiation in acid production capacity, carbon source utilization efficiency, and specific metabolite synthesis ability among the eight LAB strains but also provided a genomic theoretical basis for explaining their differences in gel formation rate, gel property changes, and flavor substance composition during soy protein gel fermentation. Future research can further focus on the expression verification of key differential genes in carbohydrate-related pathways, or combine transcriptomic and metabolomic data to deeply analyze the association mechanism between gene function and fermentation phenotype, providing more precise targets for screening dominant LAB strains suitable for soy protein gel fermentation.

### 3.4.2. Nucleotide Metabolism Pathways and Lysine/Arginine Biosynthesis Pathways

Nucleotide metabolism pathways include the purine metabolism pathway (ko00230) and the pyrimidine metabolism pathway (ko00240). The lysine/arginine biosynthesis pathways are (ko00300) and (ko00220), respectively. There are also obvious differences in the coding genes of the eight LAB strains involved in these pathways.

The purine metabolism pathway, as shown in Figure 8, is the central pathway of purine nucleotide synthesis and degradation of adenine nucleotides and guanine nucleotides, which is central to growth

and reproduction as well as adaptation to stress in the strains. The Lactobacillus plantarum possesses the largest number of coding genes that are part of this pathway (52) and Streptococcus thermophilus the least number (37). Moreover, one can draw attention to the fact that Lactobacillus acidiphilus possesses a unique coding gene of diadenosine hexaphosphate hydrolase of intracellular energy metabolism regulation Lactobacillus plantarum has unique coding genes of 3'-phosphoadenosine 5'-phosphosulfate synthase [EC:2.7.7.4 2.7.1.25], 3',5'-cyclic-nucleotide phosphodiesterase [EC: These differences in genes can result in varying capabilities of de novo purine nucleotide production and utilization efficiency of different strains, which subsequently influences the growth rate and efficiency of nucleic acids replication of these strains.

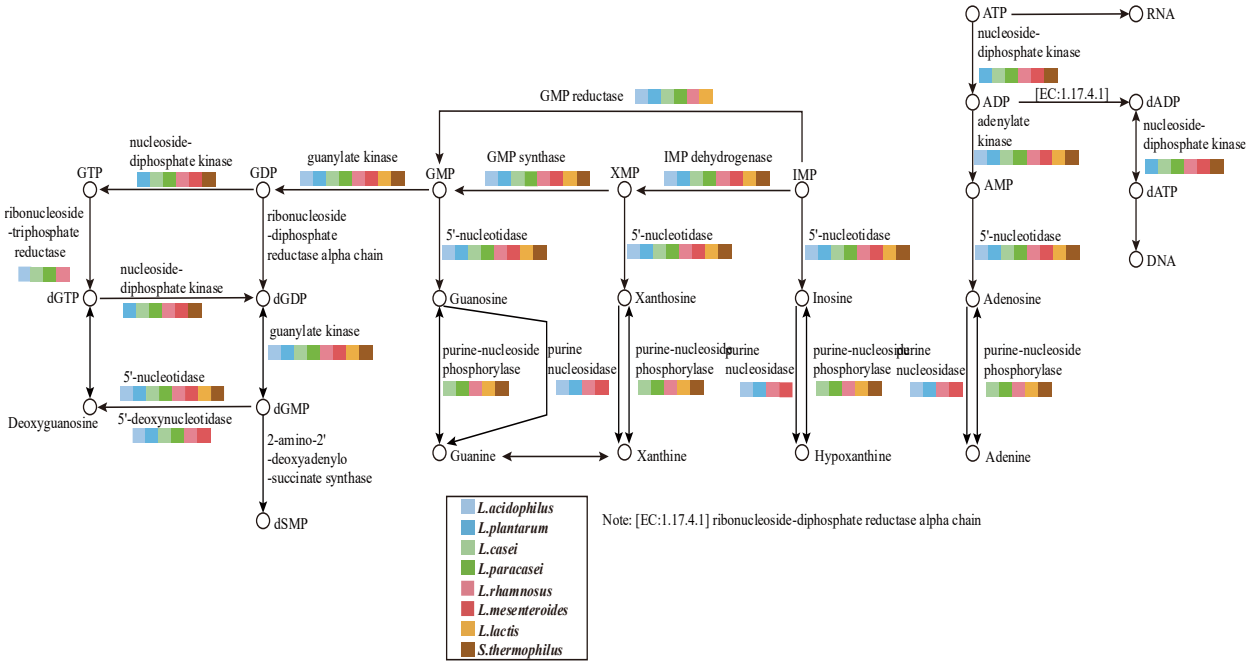


**Figure 8.** The purine metabolism.

The pyrimidine metabolism pathway, as shown in Figure 9, is mainly responsible for the de novo synthesis and salvage synthesis of pyrimidine nucleotides, and is an important pathway linking microbial metabolism and gel properties. Lacticaseibacillus rhamnosus has the most coding genes involved in this pathway, while Lactobacillus acidophilus has the least, with a difference of about 7 genes. Notably, Leuconostoc mesenteroides has unique coding genes for ribonucleoside-diphosphate reductase alpha chain [EC:1.17.4.1] and pyrimidine-specific ribonucleoside hydrolase [EC:3.2.2.-], which are involved in deoxynucleotide generation and base recycling in pyrimidine metabolism, respectively. Lactococcus lactis has a unique coding gene for carbamoyl-phosphate synthase large subunit [EC:6.3.5.5], which can encode the large subunit of carbamoyl phosphate synthase, catalyze the generation of the initial substrate for de novo pyrimidine synthesis, and is the key to pathway initiation. These genetic differences may determine the way strains obtain pyrimidine substances, affecting their survival and reproduction ability under different nutritional conditions.

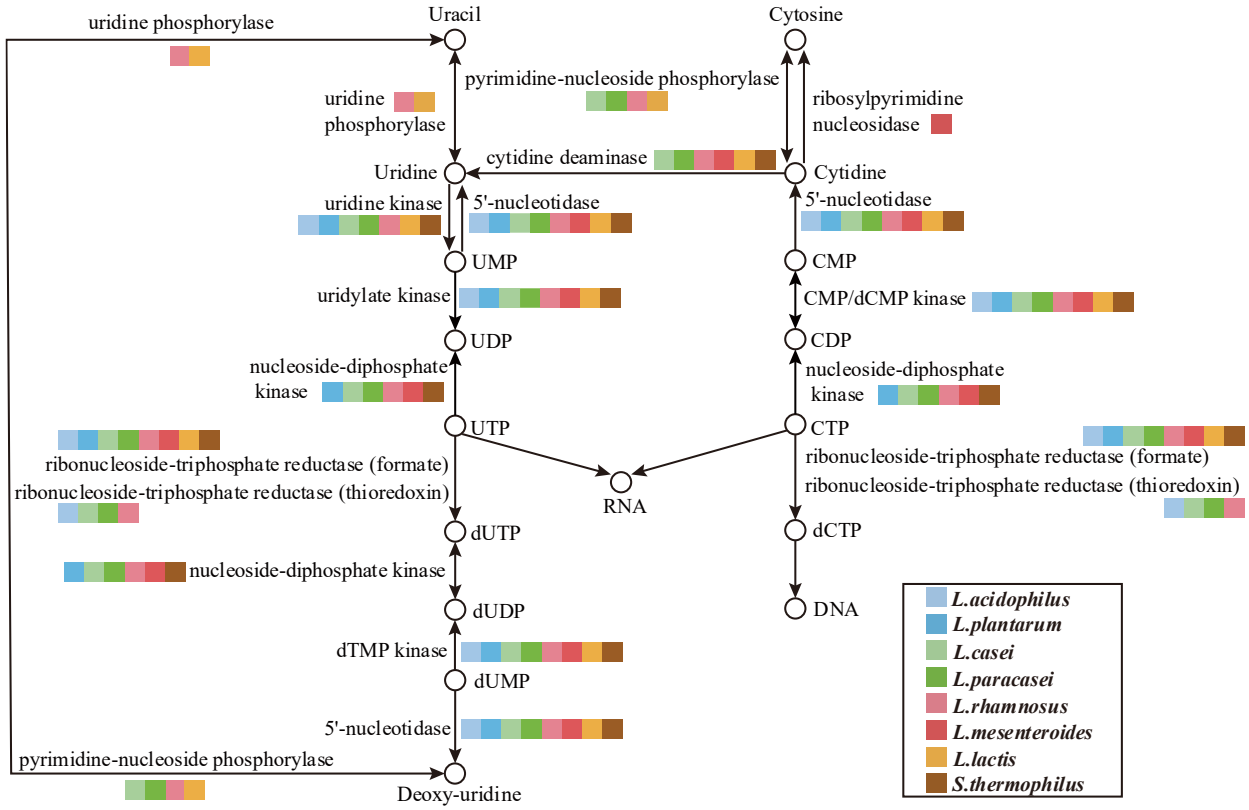


**Figure 9.** The pyrimidine metabolism.

The lysine biosynthesis pathway, as shown in Figure 10, promotes LAB division by synthesizing lysine. Its products not only serve as essential amino acids to support LAB proliferation but also participate in the structural construction of extracellular proteases and the cross-linking reaction of soy protein hydrolysis fragments, indirectly regulating gel cross-linking efficiency. Lactobacillus plantarum has the most coding genes involved in this pathway, while Lactococcus lactis and Streptococcus thermophilus have the least (only 14 pathway-annotated genes each). Notably, Lacticaseibacillus paracasei has unique coding genes for 2,3,4,5-tetrahydropyridine-2,6-dicarboxylate N-succinyltransferase [EC:2.3.1.117] and aminotransferase [EC:2.6.1.-], which can catalyze the reaction of tetrahydropyridinedicarboxylic acid with succinyl-CoA to generate N-succinyltetrahydropyridinedicarboxylic acid and catalyze the transfer of amino groups between amino acids and α-keto acids, respectively, thereby promoting the lysine synthesis process and providing essential amino acids for LAB. Leuconostoc mesenteroides has a unique coding gene for aspartate kinase [EC:2.7.2.4], which initiates essential amino acid synthesis by catalyzing the phosphorylation of aspartate to generate aspartyl phosphate. These genetic differences will affect the integrity, metabolic activity, and enzyme regulation sensitivity of the pathway, thereby being associated with bacterial proliferation efficiency, acid production capacity, and extracellular protease synthesis level, indirectly regulating the process of soy protein gel formation induced by LAB fermentation.

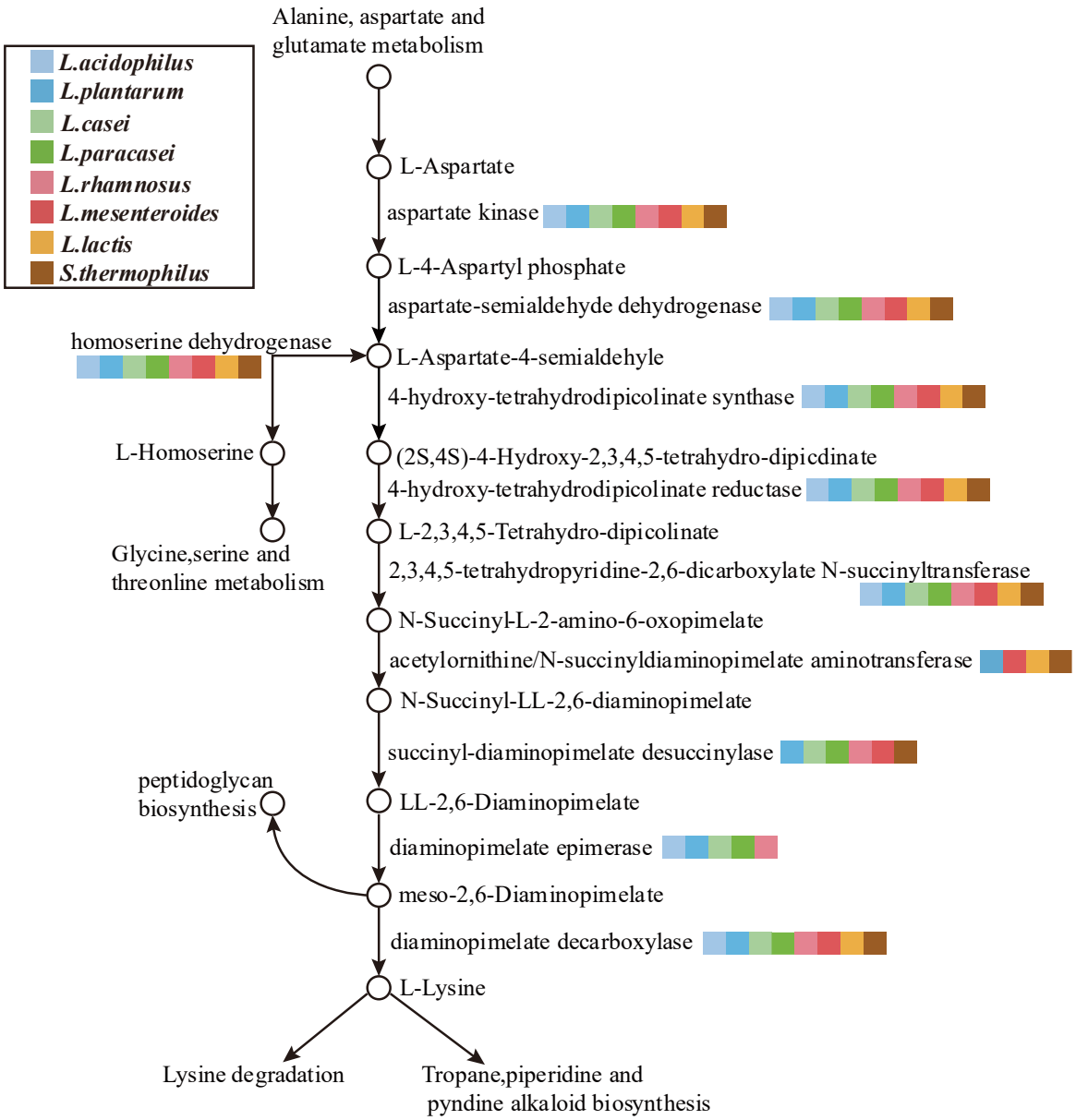


**Figure 10.** The arginine biosynthesis.

The arginine biosynthesis pathway, as shown in Figure 11, is a metabolic pathway that generates L-arginine using glutamate as the initial substrate through key enzymatic reactions such as N-acetylation modification, carbamoyl phosphate synthesis, and citrulline conversion. It is a "core power pathway" that provides key amino acid residues for proteases and promotes efficient hydrolysis of soy protein and dense formation of gel networks. Lactococcus lactis has the most coding genes involved in this pathway, while Lactobacillus acidophilus has the least. Notably, Lactobacillus acidophilus has a unique coding gene for arginase [EC:3.5.3.1], Lactobacillus plantarum has unique coding genes for argininosuccinate lyase [EC:4.3.2.1] and glutamine synthetase [EC:6.3.1.2]; Streptococcus thermophilus has unique coding genes for urease subunit alpha [EC:3.5.1.5], urease subunit beta [EC:3.5.1.5], and urease subunit gamma [EC:3.5.1.5]; in addition, Lactococcus lactis has unique coding genes for acetylornithine deacetylase [EC:3.5.1.16] and carbamoyl-phosphate synthase large subunit [EC:6.3.5.5], which can serve as key nodes and metabolic hubs for arginine synthesis, respectively, promoting its fermentation induction effect. These genetic differences will affect the growth activity, stress resistance, and extracellular protease secretion efficiency of LAB by changing the synthesis amount and supply efficiency of arginine, thereby indirectly changing their efficacy in soy protein gel fermentation.

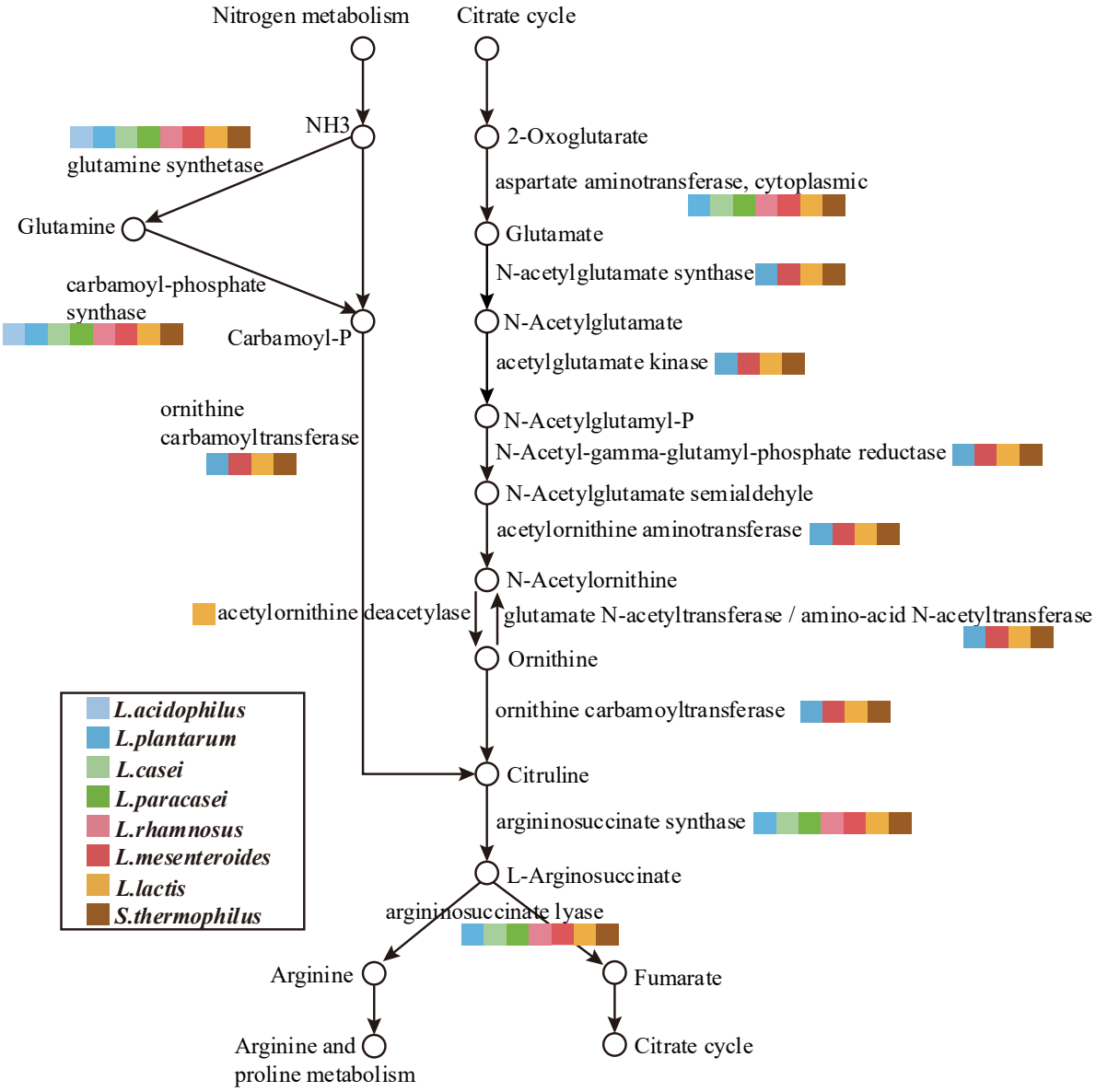


**Figure 11.** The arginine biosynthesis.

In summary, through the analysis of coding genes of eight LAB strains in four pathways (nucleotide metabolism: purine metabolism, pyrimidine metabolism, and lysine/arginine biosynthesis), this study further revealed the differentiation law of functional genes among strains: in nucleotide metabolism pathways, there were significant differences in the number of coding genes between Lactobacillus plantarum and Streptococcus thermophilus, and the existence of unique genes (such as coding genes for 3'-phosphoadenosine 5'-phosphosulfate synthase [EC:2.7.7.4 2.7.1.25]) led to obvious differences in nucleic acid synthesis efficiency and purine/pyrimidine utilization preferences among different strains; in lysine/arginine biosynthesis pathways, Lactobacillus plantarum had a relatively high number of coding genes, indicating high pathway integrity, strong synthesis ability, and good environmental adaptability. In contrast, Lactobacillus acidophilus had a small number of coding genes, resulting in weak self-synthesis ability and metabolic functions that are more dependent on the external environment, which may easily affect its reaction efficacy. These genetic differences not only affect the basic physiological activities of the eight LAB strains but also indirectly regulate their performance in inducing soy protein gel formation. For example, strains with rich lysine/arginine biosynthesis genes may have more complete synthesis pathways, making it easier to supplement amino acids in the fermentation system and promote protein degradation and gel network formation; however, the results showed that Lactobacillus plantarum had poor induction

performance, which may be due to excessive protein degradation by its proteases [29] and low EPS production [23]. In the future, functional verification can be carried out on key differential genes in amino acid biosynthesis pathways and cofactor synthesis pathways, or combined with nutrient consumption and product accumulation data during fermentation to further clarify the association between gene function and fermentation-induced gel properties, providing more comprehensive theoretical support for optimizing LAB induction formulas and improving the quality of soy protein gel products.

### 3.4.3. ABC Transporter Pathway

The ABC transporter pathway (ko02010) is the core pathway responsible for transmembrane transport of substances in microorganisms such as LAB. The ATP transporter encoded by it can realize the transmembrane uptake of essential nutrients for growth and the efflux of metabolic by-products and potential inhibitors through ATP hydrolysis for energy supply.

There are obvious differences in the number of coding genes of the ABC transporter pathway among the eight LAB strains involved: Lacticaseibacillus paracasei has the most ABC transporter coding genes (92), which can efficiently transport soy protein hydrolyzed peptides to provide nitrogen for bacteria and promote protease secretion; Streptococcus thermophilus has the least (49), with a difference of about 43 genes. In addition, it is worth noting that Lacticaseibacillus paracasei has unique ABC transporter coding genes that act as transmembrane subunits of the ABC transport system and can mediate the transmembrane entry of branched-chain amino acids produced by soy protein hydrolysis into bacteria, such as branched-chain amino acid transport system permease protein. Streptococcus thermophilus has unique coding genes for carbohydrate substrates that can efflux fermentation-produced metabolic by-products through ATP energy supply to maintain intracellular metabolic homeostasis, such as ATP-binding cassette, subfamily B, multidrug efflux pump. Lactobacillus plantarum contains ABC transporter coding genes that can mediate the transmembrane transport of macrolide substances or structurally similar metabolites through ATP energy supply, reducing the impact of potential inhibitors in the fermentation system on bacteria and maintaining their proliferation and acid production activity, such as macrolide transport system ATP-binding/permease protein. These genetic differences will significantly affect the fermentation process of bacterial species and the quality of induced gels. Unique genes further endow bacterial species with functional specificity, which may lead to significant differences in nutrient utilization preferences and stress resistance among different strains, thereby affecting their growth rate, nutrient utilization efficiency, and fermentation product stability during the induction of soy protein gel formation.

## 3.5. GO Enrichment Analysis

Through GO enrichment analysis, as shown in Table 2, it was found that the eight LAB strains (Lactobacillus acidophilus, Lactobacillus plantarum, Lacticaseibacillus casei, Lacticaseibacillus paracasei, Lacticaseibacillus rhamnosus, Leuconostoc mesenteroides, Lactococcus lactis, and Streptococcus thermophilus) had roughly similar enrichment results in three dimensions: biological process (BP), molecular function (MF), and cellular component (CC), reflecting the conservation of LAB in basic functions. In terms of biological process (BP), the eight strains mainly participated in biological process, cellular process, metabolic process, cellular metabolic process, organic substance metabolic process, primary metabolic process, nitrogen compound metabolic process, cellular nitrogen compound metabolic process, single-organism process, macromolecule metabolic process, etc.; at the molecular function level, they mainly exerted catalytic activity, transferase activity, hydrolase activity, nucleic acid binding, structural molecule activity, etc., which are the core guarantees for strains to complete energy metabolism and material transformation; at the cellular component level, the enriched genes were mainly localized in cell part, cytoplasm, macromolecular complex, intracellular organelle, intracellular ribonucleoprotein complex, membrane, ribosome, etc., which were highly matched with the locations of metabolic reactions and the action positions of functional proteins.

**Table 2.** Statistical Number of Genes Annotated in GO Biological Processes of Eight LAB Strains.

| GO pathway | *L.acidophilus* | *L.plantarum* | *L.casei* | *L.paracasei* | *L.rhamnosus* | *L.mesenteroides* | *L.lactis* | *S.thermophilus* |
|---|---|---|---|---|---|---|---|---|
| glycolytic process | 6 | 7 | 7 | 7 | 7 | 6 | 7 | 7 |
| translation | 46 | 47 | 48 | 48 | 50 | 46 | 46 | 49 |
| Proteolysis | 9 | 9 | 9 | 10 | 10 | 10 | 10 | 9 |
| protein metabolic process | 61 | 69 | 67 | 69 | 70 | 63 | 64 | 64 |
| response to extracellular stimulus | 5 | 6 | 6 | 6 | 6 | 5 | 8 | 5 |
| organic acid biosynthetic process | 18 | 46 | 29 | 33 | 32 | 42 | 49 | 42 |
| organic acid metabolic process | 37 | 64 | 48 | 51 | 53 | 58 | 69 | 60 |
| carbohydrate metabolic process | 17 | 29 | 35 | 28 | 35 | 20 | 26 | 16 |
| organic substance metabolic process | 217 | 285 | 276 | 270 | 280 | 253 | 278 | 252 |
| Monosaccharide Metabolic Process | 4 | 9 | 9 | 6 | 11 | 8 | 7 | 5 |
| Polysaccharide metabolic process | 5 | 6 | 8 | 6 | 8 | 3 | 5 | 2 |
| lipopolysaccharide metabolic process | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 1 |
| glycoprotein metabolic process | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| macromolecular complex assembly | 11 | 13 | 12 | 12 | 11 | 10 | 10 | 11 |
| extracellular polysaccharide biosynthetic process | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 |

However, there were still obvious strain differences in some GO functional terms. For example, in biological processes such as organic substance metabolic process, Lactobacillus plantarum had the most significantly differentially enriched genes (285), while Lactobacillus acidophilus had the least (217), a difference of about 1.31 times; at the molecular function level, Lactobacillus plantarum had significantly more enriched genes in terms such as total molecular function and catalytic activity than other strains, while no significant enrichment of this functional term was detected in Lactobacillus acidophilus; at the cellular component level, Lactococcus lactis had the highest enrichment degree overall, followed by Lacticaseibacillus casei, Lactobacillus plantarum, and Lacticaseibacillus rhamnosus. Enriched genes related to components such as ATP-binding cassette (ABC) transporter complex were only detected in Lactobacillus plantarum and Lacticaseibacillus casei, but not significantly enriched in other strains.

Notably, previous fermentation experiments verified that Lacticaseibacillus casei had significantly different effects on improving the formation rate of soy protein gels induced compared to other bacteria. This strain had the most enriched genes in biological processes such as lactic acid biosynthesis and glycolysis, and these genes were mostly key regulatory genes in these processes. Therefore, the efficient participation in this biological process supported the excellent performance of Lacticaseibacillus casei in soy protein gel fermentation at the functional level, and also provided GO functional evidence for analyzing the molecular mechanism of the fermentation characteristics of Lacticaseibacillus casei.

## 4. Conclusion

In summary, this study determined the texture properties of soy protein gels induced by LAB, compared the effects of eight strains on the induced gel hardness, springiness, cohesiveness, gumminess, and chewiness at different times, and analyzed the genomic information of pathways related to the induction process. The results showed that there were significant differences in the induction effects of the eight LAB strains, which were directly related to the number of pathway genes and key genes, thereby regulating the properties of soy protein gels; at the same time, it was observed that the formation of gels induced by LAB fermentation involved the coordination of multiple mechanisms, providing a basis for the subsequent analysis of the specific functions of genomes in different pathways. The results of this study can provide a reference and auxiliary anchor for further exploring the specific functions of genes related to the induction process and realizing the precise regulation of gel properties, and also help improve the application value of the gel in the food field.

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