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Structural Determinants and Stability of Frutalin Isoforms from *Artocarpus incisa*: Insights from Molecular Modeling, Docking, and Dynamics Simulations

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ARTIGO ORIGINAL

RESUMO

A frutalina (FTL) é uma lectina vegetal derivada das sementes de *Artocarpus incisa* (fruta-pão), previamente descrita por apresentar diversas atividades biológicas. Neste estudo, investigamos a variabilidade estrutural entre isoformas de FTL e os determinantes moleculares associados à sua estabilidade quaternária e às interações com ligantes. A FTL foi isolada por cromatografia de afinidade em agarose-D-galactose, e a espectrometria de massas com deconvolução revelou múltiplas espécies em torno de 16 kDa, sugerindo a presença de isoformas. Cinco modelos estruturais foram gerados a partir de sequências obtidas por RT-PCR, utilizando como molde a estrutura cristalográfica. Análises de docking molecular foram realizadas com o software HEX 8.0.0 para avaliar interações lectina–carboidrato, enquanto simulações de dinâmica molecular foram conduzidas no pacote GROMACS para investigar a estabilidade da estrutura tetramérica em meio aquoso. Os resultados indicam que resíduos específicos contribuem para a estabilização da estrutura quaternária, mantendo ligações de hidrogênio intersubunidades, enquanto a rigidez estrutural é fortemente influenciada por resíduos localizados em regiões de folhas-β. Todas as isoformas apresentaram perfis de interação semelhantes com D-galactose e D-manose, envolvendo aproximadamente oito contatos-chave por complexo, sugerindo comportamento de ligação conservado. Esses achados indicam que a variabilidade estrutural entre isoformas não altera significativamente o reconhecimento de carboidratos, evidenciando a necessidade de investigações adicionais com ligantes maiores ou mais complexos. De modo geral, este estudo demonstra o potencial de abordagens bioinformáticas integradas na elucidação das relações estrutura–função em lectinas, contribuindo para a ampliação de suas aplicações biotecnológicas.

Palavras-chave: Frutalina; lectina de *Artocarpus incisa*; bioinformática; docking

molecular; dinâmica molecular.

ABSTRACT

Frutalin (FTL) is a plant lectin derived from the seeds of Artocarpus incisa (breadfruit), previously reported to exhibit diverse biological activities. In this study, we investigated the structural variability among FTL isoforms and the molecular determinants underlying their quaternary stability and ligand interactions. FTL was isolated by affinity chromatography on D-galactose-agarose, and deconvoluted mass spectrometry revealed multiple species around 16 kDa, suggesting the presence of isoforms. Five structural models were generated based on sequences obtained by RT-PCR, using the crystallographic structure as a template. Molecular docking analyses were performed using HEX 8.0.0 to evaluate lectin–carbohydrate interactions, while molecular dynamics simulations were conducted with the GROMACS package to assess the stability of the tetrameric assembly in an aqueous environment. The results indicate that specific residues contribute to the stabilization of the quaternary structure, maintaining inter-subunit hydrogen bonding, whereas structural rigidity is strongly influenced by residues within β-sheet regions. All isoforms exhibited comparable interaction profiles with D-galactose and D-mannose, involving approximately eight key contacts per complex, suggesting conserved binding behavior. These findings indicate that structural variability among isoforms does not significantly alter carbohydrate recognition, highlighting the need for further investigations using larger or more complex ligands. Overall, this study demonstrates the potential of integrated bioinformatics approaches to elucidate structure–function relationships in lectins, contributing to the expansion of their biotechnological applications.
Keywords: Frutalin, *Artocarpus incisa* lectin, Bioinformatics, Molecular Docking, Molecular Dynamics.

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1 INTRODUCTION

Lectins are a diverse class of carbohydrate-binding proteins capable of selectively recognizing specific glycan structures without altering their covalent configuration. These proteins are widely distributed in nature and play essential roles in biological processes such as cell–cell recognition, immune response modulation, and host–pathogen interactions (Moreira et al., 1998; Lobo et al., 2017). In recent years, lectins have also attracted significant attention due to their broad biotechnological and biomedical applications, including antimicrobial, antiviral, and antitumor activities, as well as their use in glycoprotein purification and molecular recognition studies (Araujo et al., 2018; Lobo et al., 2017).

Frutalin (FTL) is a plant lectin obtained from the seeds of *Artocarpus incisa* (breadfruit), typically isolated by affinity chromatography on D-galactose-agarose columns (Monteiro-Moreira, 2002). Deconvoluted mass spectrometry analyses have revealed multiple molecular species around 16 kDa, suggesting the presence of distinct isoforms (Vieira-Neto et al., 2018). These isoforms may differ in subtle structural features that influence their stability and carbohydrate-binding properties.

The genus *Artocarpus* (*Moraceae*) comprises approximately 50 species, several of which produce lectins that have been isolated and structurally characterized. Among them, jacalin, derived from *Artocarpus integrifolia*, represents one of the most extensively studied lectins of this family, serving as a structural and functional reference for related proteins (Moreira and Ainouz, 1977). Lectins from this genus share a conserved β-prism fold, although variations in amino acid composition may lead to differences in oligomerization and ligand specificity.

Artocarpus incisa, also known as *Artocarpus altilis*, is a tropical species widely

distributed in Brazil and other subtropical regions. It produces two main fruit varieties, including a seed-bearing type that represents the primary source of frutalin (Figure 1). The availability of this lectin and its structural similarity to other well-characterized members of the Jacalin-related lectin family make it a suitable model for investigating structure–function relationships in plant lectins.

Figure 1. Leaf and fruit of *Artocarpus incisa*, freshly collected after ripening, in Maranguape-CE.

Source: author

Early studies on the seed-bearing variety of *Artocarpus incisa* led to the isolation of a galactose-binding lectin later termed frutalin (Moreira and Oliveira, 1983; Moreira et al., 1998). Frutalin is a glycoprotein with specificity primarily toward α-D-galactose, while also recognizing epimers such as α-D-mannose. Structurally, it is composed of α- and β-chains arranged into a tetrameric assembly stabilized by non-covalent interactions, with no evidence of disulfide bonds (Monteiro-Moreira, 2002).

Mass spectrometry analyses have consistently revealed multiple molecular species

around 16 kDa, supporting the presence of isoforms (Monteiro-Moreira et al., 2015; Vieira-Neto et al., 2018). These isoforms arise primarily from natural heterogeneity and sequence variability, which can impact structural stability and biological activity. Despite high similarity to jacalin-related lectins, subtle sequence variations may influence oligomerization behavior and ligand-binding properties (Nepomuceno, 2008).

The quaternary structure of frutalin is strongly influenced by environmental conditions, particularly pH and ligand presence. Previous studies have demonstrated that carbohydrate binding plays a key role in stabilizing the tetrameric assembly, especially under conditions that would otherwise favor dissociation (Monteiro-Moreira, 2002; Campana et al., 2002). These findings highlight the dynamic nature of frutalin and reinforce the importance of ligand-mediated stabilization in lectin function.

Recent structural investigations have provided new insights into the molecular basis of carbohydrate recognition in frutalin and related lectins, revealing conserved features of the β-prism fold and the structural determinants of anomeric specificity (Vieira-Neto et al., 2018). These advances underscore the relevance of integrating structural and computational approaches to better understand lectin–carbohydrate interactions.

Despite extensive biochemical characterization, the structural and functional implications of isoform variability in frutalin remain insufficiently explored. In particular, the extent to which sequence variations affect quaternary stability and ligand interaction profiles is not fully understood.

In this context, the present study aims to investigate the structural nuances that differentiate frutalin isoforms and to identify the key molecular determinants responsible for stabilizing its quaternary structure, combining molecular modeling, docking, and molecular dynamics simulations.

2 METHODS

2.1. Partial characterization of frutalin isoforms by two-dimensional electrophoresis

The protein profile of frutalin (FTL) isoforms was initially assessed by two-dimensional gel electrophoresis (2-DE), combining isoelectric focusing (IEF) and SDS-PAGE, a well-established approach for resolving complex protein mixtures based on isoelectric point (pI) and molecular mass (O'Farrell, 1975). Lyophilized FTL (10 mg) was solubilized in a denaturing buffer containing 7 M urea and 2 M thiourea, and protein concentration was determined using the Bradford method (Calvete et al., 1998).

For 2-DE analysis, 300 µg of protein were loaded onto immobilized pH gradient (IPG) strips (pH 3–10, 13 cm), followed by passive rehydration for 16 h. IEF was performed using a stepwise voltage program up to a total of 18,000 Vh at 20 °C. After focusing, strips were equilibrated in SDS-containing buffer with dithiothreitol and subsequently alkylated with iodoacetamide prior to second-dimension separation on 17.5% polyacrylamide gels. Protein spots were visualized by colloidal Coomassie Brilliant Blue staining.

2.2. Spot selection and in-gel digestion

Gels were scanned and analyzed using ImageMaster 2D Platinum software (GE Healthcare) for spot detection, quantification, and estimation of pI and molecular mass. Selected protein spots were manually excised and subjected to in-gel digestion with trypsin following established protocols (Hellman et al., 1995). Briefly, gel pieces were destained, dehydrated, and rehydrated with trypsin solution, followed by overnight digestion at 37 °C. Peptides were extracted using acetonitrile and trifluoroacetic acid prior

to mass spectrometry analysis.

2.3. Mass spectrometry analysis

Peptide mixtures were analyzed using a SYNAPT HDMS mass spectrometer (Waters, Manchester, UK) coupled to a nanoUPLC-ESI system. Samples were separated by reverse-phase chromatography using a gradient of acetonitrile in 0.1% formic acid at a flow rate of 300 nL/min. Mass spectra were processed using maximum entropy deconvolution (MaxEnt) to obtain resolved mass profiles (Ferrige and Seddon, 1991).

2.4. Molecular modeling

Three-dimensional structures of the main FTL isoforms were modeled based on amino acid sequences obtained by RT-PCR (Nepomuceno, 2008), using the crystallographic structure (PDB ID: 4WOG) as a template. Homology modeling was performed using the SWISS-MODEL server (Kelley et al., 2009), generating structurally refined models for subsequent analyses.

2.5. Molecular docking and dynamics simulations

Ligand-binding affinity toward α-D-galactose was evaluated by molecular docking. Ligand preparation was performed using Open Babel (O'Boyle et al., 2011), while receptor structures were prepared using AutoDock Tools (Morris et al., 2009). Polar hydrogens and Kollman charges were assigned, and structures were converted to PDBQT format.

Docking simulations were carried out using a grid box centered at coordinates x = −45.0, y = 60.0, and z = 12.0, with dimensions of 50 Å in each direction and an exhaustiveness parameter of 64. Ten independent runs were performed, and resulting clusters were evaluated based on binding energy (kcal/mol) and root mean square

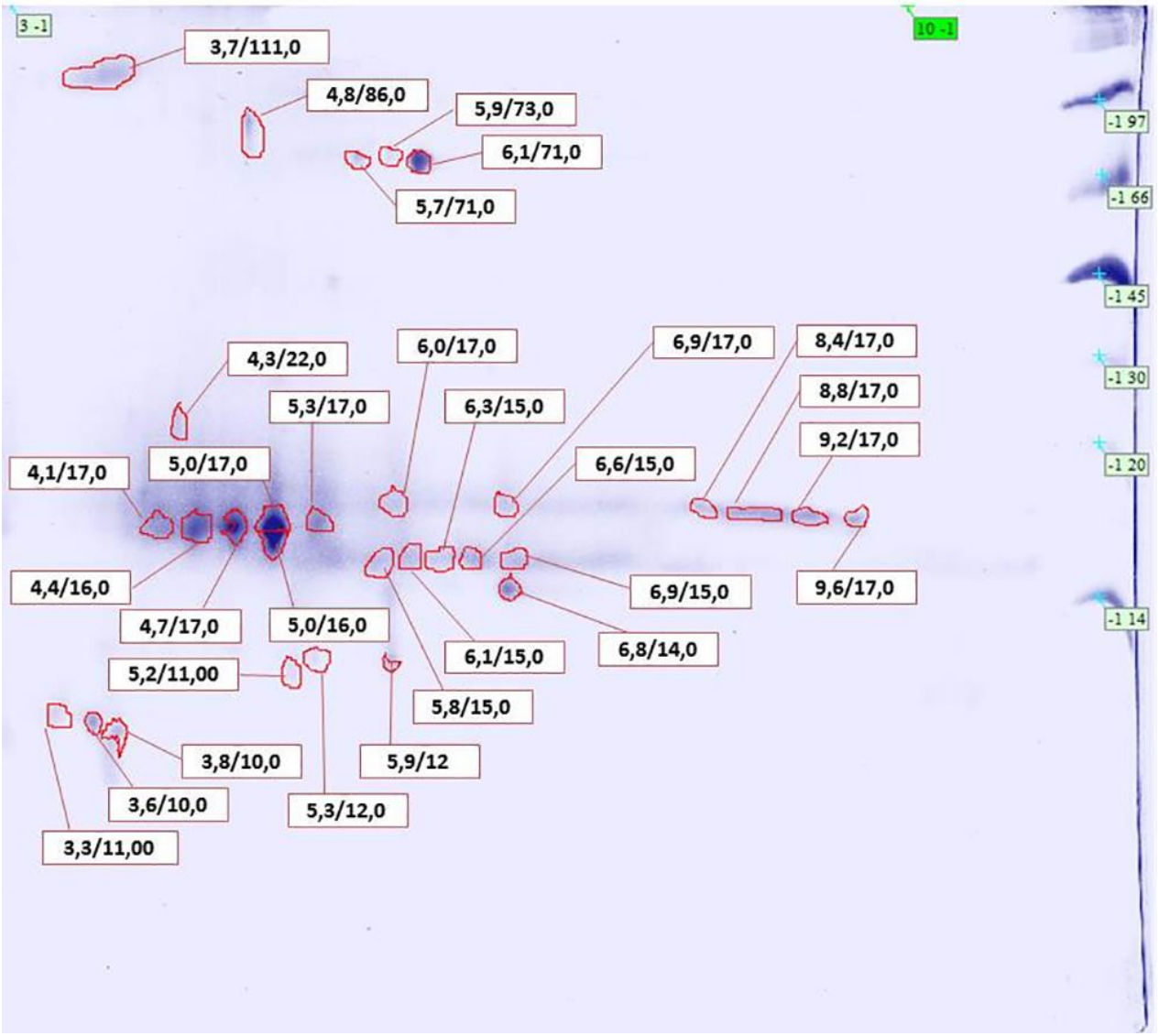
deviation (RMSD).

Structural analysis of docking poses was conducted using PyMOL (DeLano, 2015). In addition, molecular dynamics simulations were performed using the GROMACS package (Abraham et al., 2015) to assess the stability of the tetrameric FTL structure in an aqueous environment.

3 RESULTS AND DISCUSSION

Two-dimensional electrophoresis (2-DE) provided an overview of the isoform distribution of frutalin (FTL), revealing a heterogeneous protein pattern. Multiple spots with varying intensities were detected, predominantly within the molecular mass range of 12–16 kDa (Figure 2), consistent with previously reported values for frutalin subunits (Vieira-Neto et al., 2018).

Figure 2. Two-dimensional electrophoresis (2-DE) profile of frutalin (FTL). Proteins were separated by isoelectric focusing followed by SDS-PAGE (15%) and visualized by colloidal Coomassie Brilliant Blue G-250 staining. Multiple protein spots are observed predominantly in the 12–16 kDa range, indicating the presence of isoforms with distinct isoelectric points.



Source: Authors.

The distribution of spots across the gel, particularly along the isoelectric focusing axis, indicates the presence of isoforms differing in charge properties, likely reflecting sequence variability and/or post-translational modifications. This heterogeneity supports mass spectrometry findings and reinforces the existence of structurally distinct FTL variants.

Spots were detected and analyzed using a combination of automated and manual approaches, as described in Section 2.1, allowing reliable estimation of molecular mass and isoelectric point for subsequent proteomic characterization.

Analysis of the 2-DE maps revealed distinct isoelectric points and molecular

masses among the detected spots, confirming that proteins migrating within the 12–16 kDa range correspond to different frutalin (FTL) isoforms, consistent with the characteristic banding pattern observed in conventional SDS-PAGE.

All spots were subjected to ESI-MS analysis following reverse-phase UPLC separation. Peptide profiling confirmed that all identified proteins correspond to frutalin, supporting the presence of multiple isoforms rather than distinct proteins.

The observed heterogeneity is likely associated with sequence variability among isoforms, as previously reported for lectins from *Artocarpus* species (Nepomuceno, 2008). Such variability may contribute to subtle differences in structural stability and ligand recognition, reinforcing the functional relevance of isoform diversity.

Given that mature seeds were used as the protein source, the predominance of specific isoforms may reflect stage-dependent expression patterns, which could influence the structural properties of the purified lectin. This aspect is particularly relevant for crystallographic studies, as the dominant isoform is more likely to be represented in the solved structure (PDB ID: 4WOG).

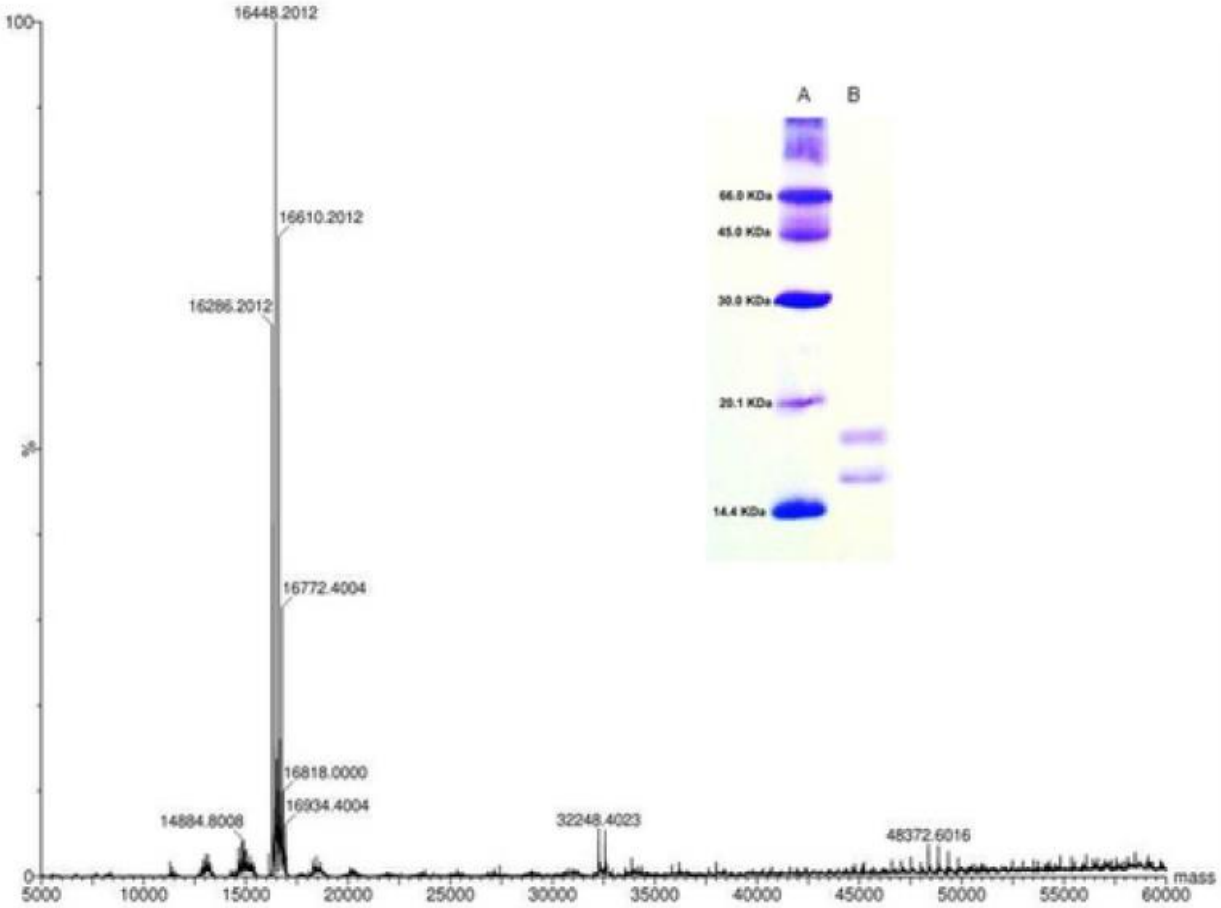
Overall, the combined proteomic and electrophoretic analyses provide consistent evidence for the existence of frutalin isoforms and highlight their potential impact on structure–function relationships in this lectin family.

Additional evidence supporting the presence of frutalin (FTL) isoforms was obtained from SDS-PAGE and mass spectrometry analyses. The electrophoretic profile revealed a characteristic lectin pattern consisting of two bands at approximately 15.5 and 12 kDa (Figure 2), consistent with previous reports for jacalin-related lectins (Oliveira et al., 2008). These bands are typically associated with glycosylated and less glycosylated (or non-glycosylated) forms, respectively (Monteiro-Moreira, 2002).

Deconvoluted ESI-MS spectra (Figure 2) further confirmed the heterogeneity of

the sample, revealing multiple molecular species centered around 16 kDa. This profile supports the presence of isoforms derived from the same monomeric unit rather than contamination by unrelated proteins, indicating a high degree of sample purity despite intrinsic microheterogeneity (Vieira-Neto et al., 2018).

Figure 2. SDS-PAGE and ESI-MS characterization of purified frutalin (FTL): SDS-PAGE analysis reveals two bands at approximately 15.5 and 12 kDa, consistent with different glycosylation states; Deconvoluted ESI-MS spectra show multiple molecular species centered around 16 kDa, confirming the presence of isoforms derived from the same protein.



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The coexistence of isoforms may arise from sequence variability and/or post-translational modifications, both of which can influence structural organization and

functional properties. Although recombinant expression systems can improve protein homogeneity, the use of native frutalin remains relevant for preserving biologically meaningful structural features.

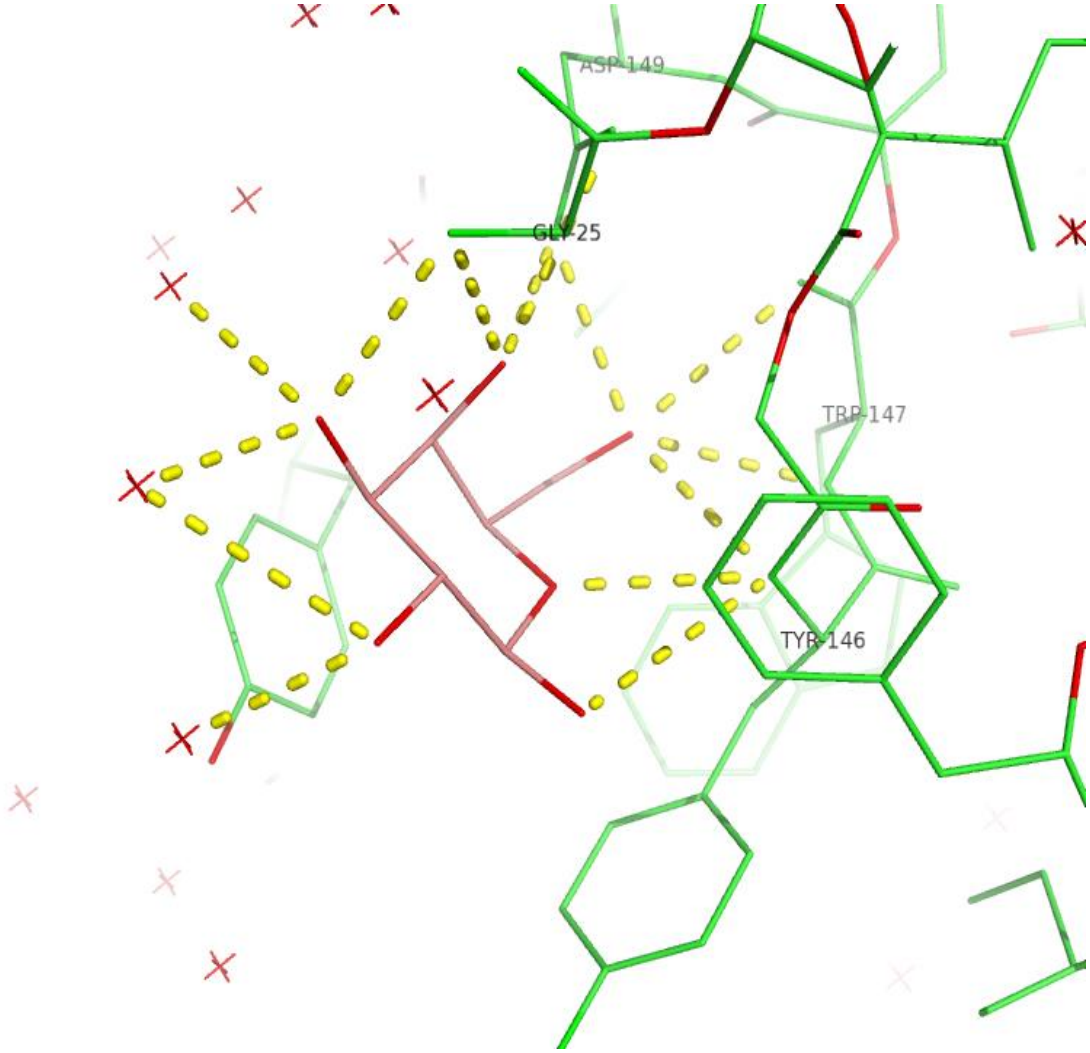
Overall, the combined SDS-PAGE and ESI-MS data demonstrate that the purified FTL preparation consists of structurally related isoforms, providing a suitable and representative system for subsequent structural and computational analyses.

Following structural characterization, the interaction profile of α-D-galactose was analyzed in the most abundant FTL isoform (clone 4.3), whose three-dimensional structure was experimentally determined (PDB ID: 5BN6). The ligand is accommodated within the carbohydrate recognition domain (CRD) through a well-defined hydrogen-bonding network involving key residues. Specifically, hydroxyl groups of the galactose moiety establish interactions with Tyr146, Gly25, Asp149, and Trp147, contributing to precise ligand positioning and stabilization within the binding pocket (Figure 3). These interactions define a conserved recognition pattern consistent with other jacalin-related lectins.

In addition to direct protein–ligand contacts, structured water molecules play a relevant role in stabilizing the complex. These water-mediated interactions contribute to the formation of hydrogen-bonding bridges between the ligand and the protein, reinforcing binding specificity and conformational stability (Weis and Drickamer, 1996) (Table 1).

The extensive interaction network observed in the CRD is consistent with the high affinity of frutalin for galactose and supports its well-documented carbohydrate-binding and hemagglutination properties.

Figure 3. Carbohydrate recognition domain (CRD) of frutalin in complex with α-D-galactose (PDB ID: 5BN6). The protein backbone is shown in green, the ligand in red, and hydrogen bonds are indicated in yellow. Structured water molecules involved in ligand stabilization are represented as red crosses, highlighting their role in mediating protein–ligand interactions.



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O número total de interações entre uma lectina e o ligante é um dos fatores principais para a energia de ligação, uma vez que um número maior levaria a uma maior

energia de interação (COZZINI e DOTTORINI, 2004).

Table 1. Detailed interaction profile between α-D-galactose and the carbohydrate recognition domain (CRD) of frutalin (PDB ID: 5BN6). The table summarizes hydrogen-bond interactions between ligand hydroxyl groups and key amino acid residues, including interaction distances (Å). Water-mediated contacts are also indicated, highlighting the contribution of structured water molecules to ligand stabilization within the binding site.

α-D-Galactose	Residue (FTL)	Bond (Å)
C1-OH	Tyr146	**3,4**
C2-OH	W1 / W2	**3,0 / 3,5**
C3-OH	Gly25	**2,9 / 3,0 / 2,8**
C3-OH	W2 / W3	**3,0 / 2,8**
C4-OH	Gly25	**2,9**
C4-OH	Asp149	**3,2**
C4-OH	Asp149	**2,6**
C6-OH	Tyr146	**3,1**
C6-OH	Trp147	**2,9**
C6-OH	Trp147	**3,1**
C6-OH	Asp149	**2,8**

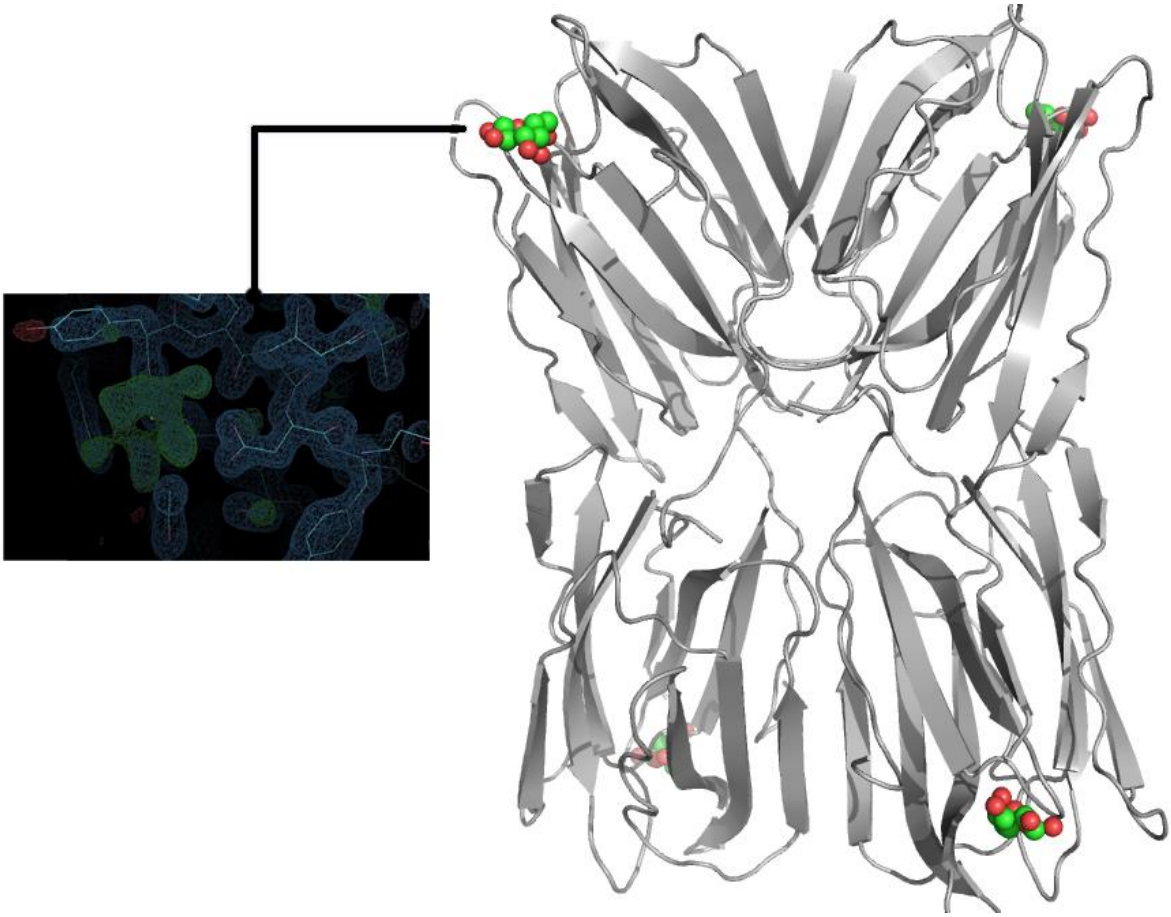
Source: author

Analysis of the spatial dimensions of the binding site reveals that the carbohydrate recognition domain (CRD) of frutalin is considerably larger than the α-D-galactose

molecule (Figure 4). This structural feature suggests that the binding pocket is adapted to accommodate more complex glycoconjugates, rather than simple monosaccharides.

Such an expanded binding interface enables additional stabilizing interactions, including multiple hydrogen bonds and van der Waals contacts, which are typically enhanced in larger ligands presenting exposed carbohydrate moieties. This observation is consistent with the reported preference of frutalin for glycosylated macromolecules over monosaccharides (Oliveira, 2009), supporting a binding mechanism driven by increased interaction surface and structural complementarity.

Figure 4. Tetrameric structure of frutalin in complex with α-D-galactose. The inset highlights the carbohydrate recognition domain (CRD), showing the ligand-binding region and the corresponding electron density map, illustrating the spatial accommodation of the ligand within the binding pocket.



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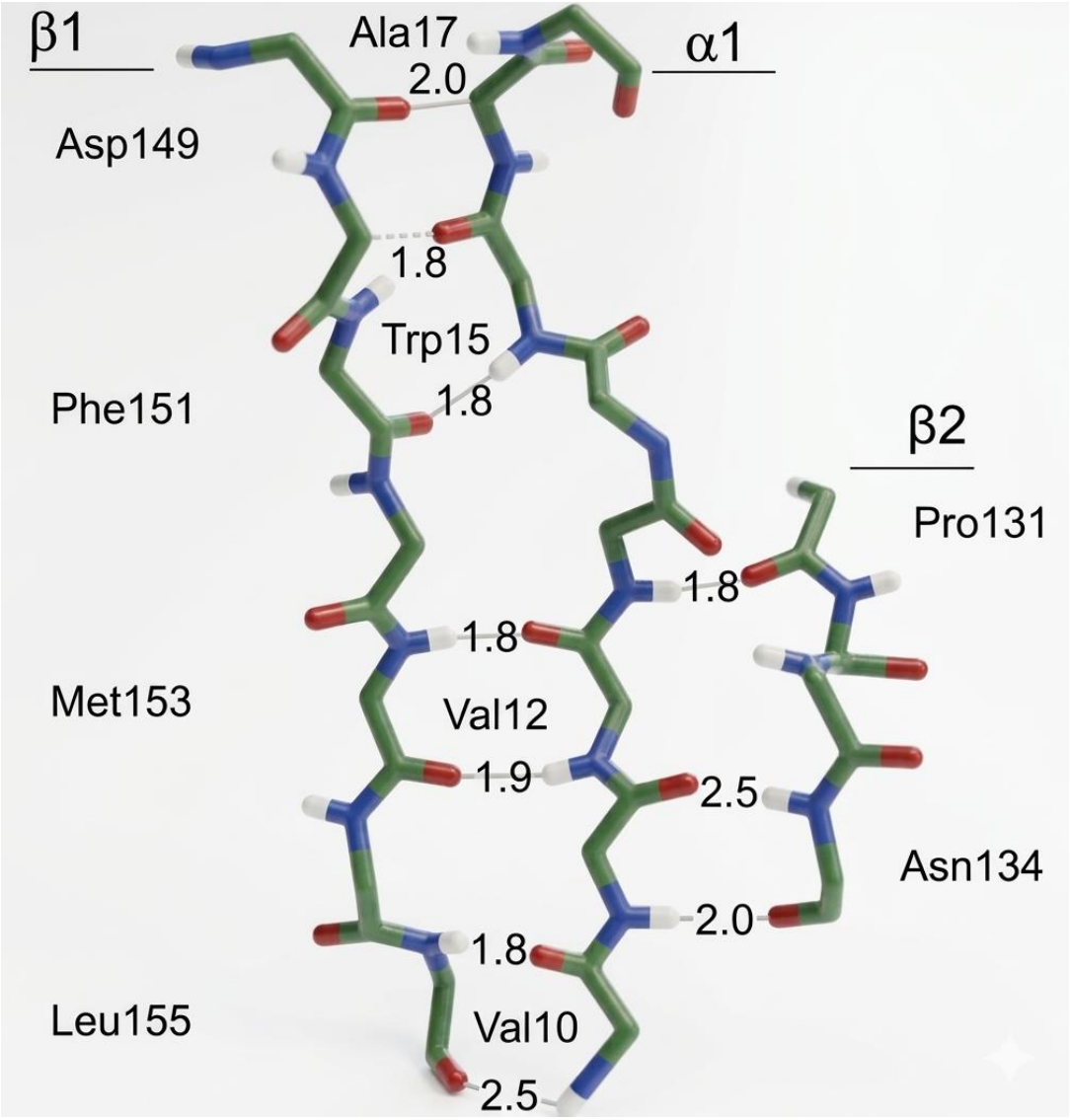
Molecular dynamics simulations indicate that frutalin exhibits a structurally stable tetrameric organization, supported by specific residue interactions that contribute to subunit stabilization. The segment spanning residues 10–19 of the α-chain (VIVGPWGAQ), enriched in hydrophobic side chains, plays a key role in maintaining structural integrity through hydrophobic packing at the subunit interface.

In addition, residues from the β-chain contribute significantly to the overall rigidity of the protein by participating in an extended network of hydrogen bonds and inter-subunit contacts. This cooperative interaction pattern enhances the stability of the quaternary structure, preserving the spatial arrangement required for ligand recognition (Figure 5).

Figure 5. Structural determinants of frutalin tetramer stabilization. Key amino acid residues involved in inter-subunit interactions are highlighted, including hydrophobic regions at the α-chain interface and hydrogen-bonding networks contributed by β-chain residues, illustrating their role in maintaining quaternary structure stability.



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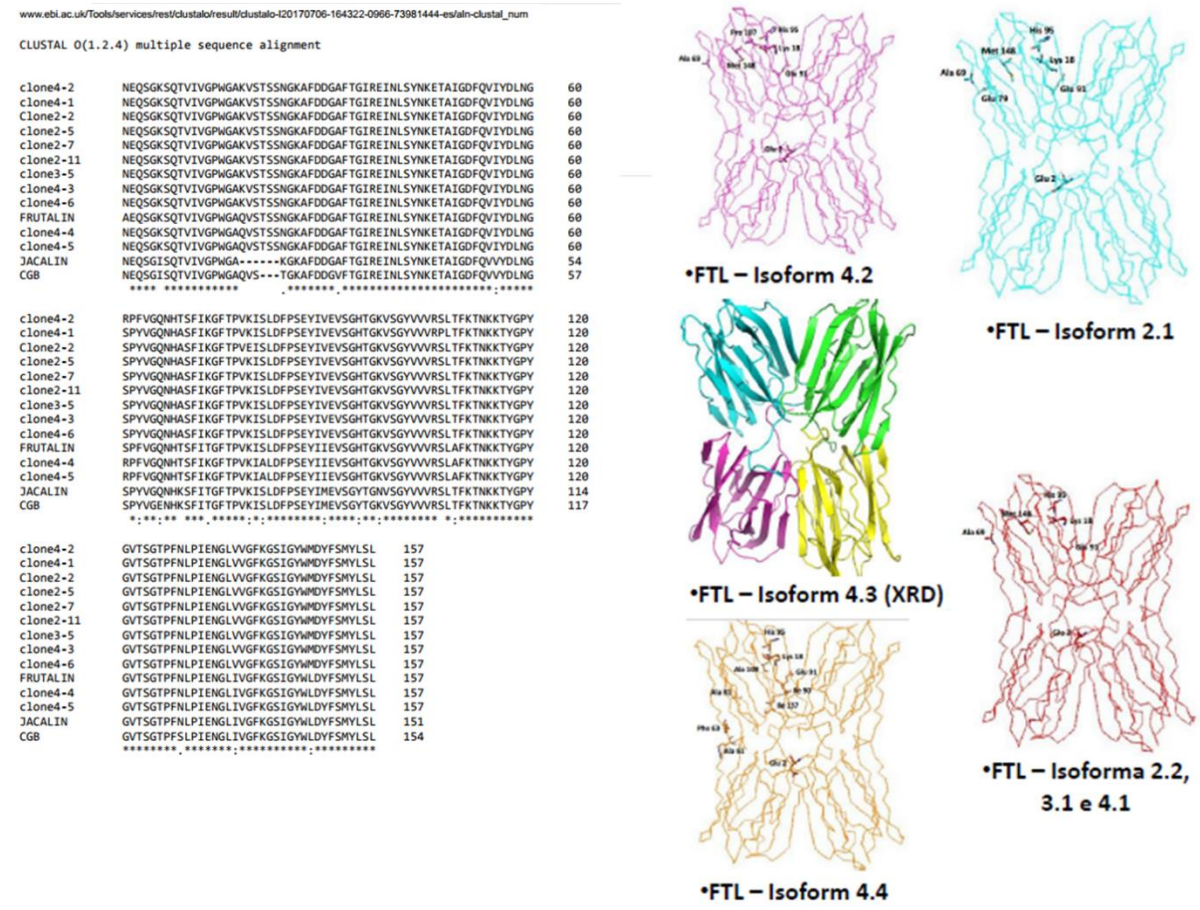
Regarding ligand interactions, both α-D-galactose and D-mannose exhibited consistent binding profiles across the analyzed FTL isoforms. Approximately eight hydrogen-bonding and polar interactions were identified within the carbohydrate recognition domain (CRD) for each isoform, indicating a conserved interaction pattern (Figure 6).

Figure 6. Sequence alignment of frutalin isoforms obtained by RT-PCR (Nepomuceno, 2008) and corresponding three-dimensional models (right) generated based on the

crystallographic structure (PDB ID: 4WOG). The models highlight the structural conservation among isoforms, particularly within the carbohydrate recognition domain (CRD), supporting their similar ligand-binding profiles.



Source: Authors.

Despite sequence variations among isoforms, no significant differences in binding affinity were observed between the ligands, suggesting that the core carbohydrate-binding mechanism is structurally preserved. This conservation is consistent with the maintenance of key residues within the CRD responsible for ligand recognition.

The similar interaction profiles observed for monosaccharides indicate that subtle structural differences among isoforms are not sufficient to markedly affect binding under these conditions.

These findings support the hypothesis that larger glycoconjugates, capable of establishing additional contacts beyond the conserved CRD, may provide enhanced binding specificity and affinity.

4 CONCLUSION

This study provides a comprehensive structural and computational characterization of frutalin (FTL) isoforms, integrating experimental and in silico approaches to elucidate the molecular determinants underlying their stability and ligand-binding behavior.

The results demonstrate that FTL is naturally expressed as a mixture of structurally conserved isoforms, whose carbohydrate recognition domains (CRDs) retain a highly preserved binding architecture. This structural conservation is reflected in the similar interaction profiles observed for α-D-galactose and D-mannose, indicating that core ligand recognition mechanisms are maintained despite sequence variability.

Molecular docking and structural analyses revealed that ligand binding is stabilized by a well-defined network of hydrogen bonds and water-mediated interactions, while molecular dynamics simulations highlighted the contribution of hydrophobic packing and inter-subunit contacts to the stability of the tetrameric structure. In particular, residues from both α- and β-chains play complementary roles in maintaining structural integrity and functional competence.

Importantly, the spatial organization of the binding site suggests an intrinsic capacity to accommodate more complex glycoconjugates, supporting the hypothesis that ligand size and multivalency may significantly enhance binding affinity and specificity.

Taken together, these findings provide new insights into the structural basis of frutalin isoform functionality and reinforce the relevance of integrating crystallographic,

bioinformatic, and molecular simulation approaches to advance the understanding of lectin–carbohydrate interactions. This work contributes to the rational exploration of frutalin as a promising scaffold for biotechnological and biomedical applications.

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