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Carbohydrate Structure and Role

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Abstract

Carbohydrates are essential biomolecules that play a variety of structural and functional roles in living organisms. As one of the three major macronutrients, along with proteins and fats, carbohydrates are a vital energy source and metabolic fuel. However, carbohydrates contribute much more than just calories. This review provides an in-depth examination of carbohydrate chemistry, structure, function, and metabolism. Focus is given to how the specific molecular structures of different carbohydrate classes including monosaccharides, disaccharides, oligosaccharides, and polysaccharides determine their physiological activities. Key topics covered include carbohydrate digestion and absorption, glycoprotein and glycolipid synthesis, energy storage, and cell signaling roles. Special attention is paid to glucose metabolism and homeostasis due to the critical importance of blood sugar regulation. Potential links between carbohydrate structures and the development of metabolic disorders are also discussed. Tables and figures are provided to illustrate key concepts and summarize important information. Current areas of research and future directions are highlighted to demonstrate how continued elucidation of carbohydrate structural chemistry may lead to improved understanding of carbohydrate biology and better therapeutic interventions for carbohydrate-related diseases. This broad review provides a structural perspective to improve comprehension of the diverse functional roles of carbohydrates in biological systems.

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1. INTRODUCTION

Carbohydrates are a vital class of biomolecules that play numerous critical roles across all domains of life. As their name indicates, carbohydrates are hydrate carbon compounds that contain carbon, hydrogen, and oxygen atoms. The basic molecular formula for carbohydrates is (CH2O)n where n is at least 3. Carbohydrates are synthesized by plants through photosynthesis and serve as the primary metabolic fuel utilized by cells to produce energy through cellular respiration [1]. In addition to their well-established function as an energy source, carbohydrates have many other important structural and functional roles. They contribute to cell membrane structure, facilitate cellular recognition, provide protection and support, and participate in numerous biological processes as activating or signaling molecules [2].

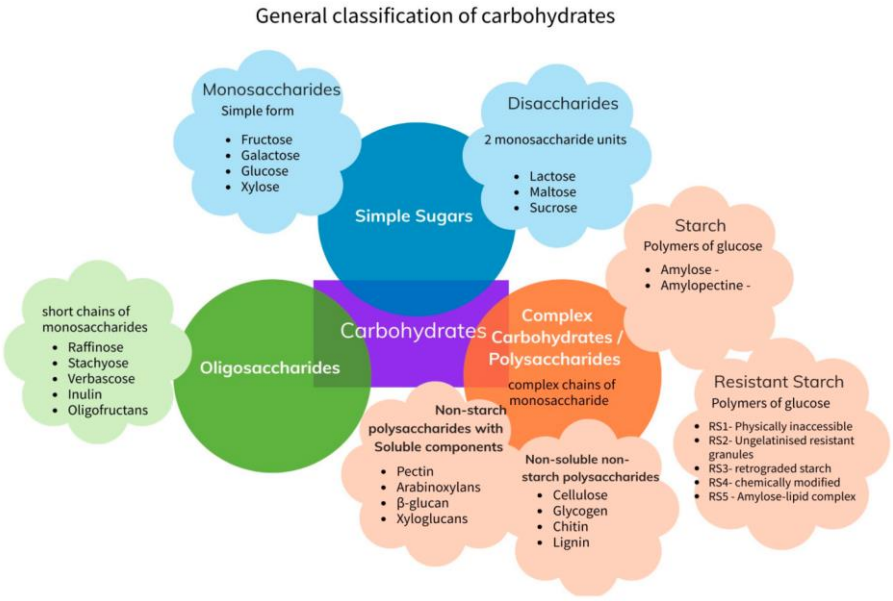

Figure 1: General classification of carbohydrates

With such widespread involvement in living systems, a thorough understanding of carbohydrate chemistry and structure is essential. The diverse physiological functions of carbohydrates are directly determined by their underlying molecular structures. Even subtle differences in molecular configuration can have significant impacts on carbohydrate metabolism and activity. Therefore, this review provides an in-depth examination of carbohydrate structure-function relationships. Focus is given to how the specific molecular

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structures of different carbohydrate classes and functional groups contribute to their biological roles.

Carbohydrates can be divided into four primary categories: monosaccharides, disaccharides, oligosaccharides, and polysaccharides. Monosaccharides are the simplest and smallest carbohydrates. They cannot be further hydrolyzed to smaller carbohydrates and serve as the building blocks for all higher order carbohydrate structures. Disaccharides contain two monosaccharide units, oligosaccharides three to ten, and polysaccharides more than ten monosaccharide units linked together [3]. Each carbohydrate category contains distinct subgroups with unique structural attributes that determine their functional capabilities.

This review will provide a thorough overview of carbohydrate chemistry starting with monosaccharide structure. Key carbohydrate classes will be covered highlighting how their molecular configurations give rise to specific biological activities. Important physiological processes involving carbohydrates such as digestion, nutrient absorption, energy metabolism, glycoprotein synthesis, cell signaling, and disease development will be discussed throughout to demonstrate the form-function relationships of carbohydrate structures. Tables and figures will be incorporated to summarize key information and illustrate structural concepts. The goal is to provide a comprehensive structural perspective to improve understanding of the varied functional roles of carbohydrates in biological systems.

2. MONOSACCHARIDE STRUCTURE AND FUNCTION

Monosaccharides are the most basic carbohydrate units. They contain a single polyhydroxy aldehyde or ketone unit making them the simplest form of a sugar molecule. Monosaccharides are further classified by the number of carbon atoms they contain which is typically three to seven carbons long. The most abundant monosaccharides relevant to human physiology are the hexoses, which contain six carbon atoms [4].

The six carbon hexoses share a common chemical formula of C6H12O6. However, they can exist as different structural isomers depending on the position of the carbonyl group within the carbon chain and the spatial arrangements around asymmetric carbons. These

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subtle structural differences confer each hexose with unique chemical properties that determine their physiological functions (See Table 1).

Table 1. Structures and functions of common hexose monosaccharides.

Monosaccharide	**Primary Functions**
Glucose	Major energy source, metabolic intermediate
Galactose	Component of lactose, glycoproteins, glycolipids
Fructose	Sweetener, glycolysis intermediate
Mannose	Component of glycoproteins, glycolipids

Glucose is the most abundant monosaccharide in nature and the primary product of photosynthesis [5]. As such, glucose plays a central role in carbohydrate metabolism and bioenergetics. Glucose in its ring form can exist in either an α-pyranose or β-pyranose structure which interconvert through mutarotation. These two anomers differ in the position of the hydroxyl group on the anomeric carbon. This structural flexibility of glucose allows it to adopt different conformations required to fit into active sites of metabolic enzymes and transport proteins [6].

Fructose and galactose are structural isomers of glucose. Fructose, also known as fruit sugar, differs from glucose only in the position of the hydroxyl group on carbon 2. This subtle change causes fructose to be much sweeter than glucose and gives it distinct metabolic properties. Fructose is metabolized independently of insulin by the liver which can lead to adverse effects when consumed in excess [7]. Galactose differs from glucose in the configuration around carbon 4 which is critical for its role in lactose synthesis and incorporation into glycoproteins and glycolipids.

Mannose is an epimer of glucose, meaning it differs only in the stereochemistry around one carbon. This C2 epimerization causes mannose to be metabolically inert compared to glucose. Instead of energy metabolism, mannose is primarily utilized for protein glycosylation [8]. Overall, the distinct structures of the various hexoses enable each one to play unique

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biological roles critical to health. Further elucidation of monosaccharide structure-function relationships will provide key insights into improving carbohydrate metabolism and preventing metabolic disorders.

3. DISACCHARIDE STRUCTURE AND FUNCTION

Disaccharides are composed of two monosaccharide units linked together by a glycosidic bond. The particular monosaccharides joined and type of glycosidic linkage determine the classification and function of each disaccharide. The four main disaccharides relevant to human nutrition are sucrose, lactose, maltose, and trehalose (See Table 2).

Table 2: Structures and functions of common dietary disaccharides.

Disaccharide	Linkage	Primary Functions
Sucrose	α-D-glucose, β-D-fructose, 1→2 glycosidic bond	Sweetener, energy source
Lactose	β-D-galactose, β-D-glucose , 1→4 glycosidic bond	Primary sugar in milk, probiotic
Maltose	α-D-glucose, α-D-glucose , 1→4 glycosidic bond	Product of starch digestion
Trehalose	α-D-glucose, α-D-glucose , 1→1 glycosidic bond	Energy storage, stress protection

Sucrose, also known as table sugar, is composed of glucose and fructose bonded together. This makes sucrose very sweet and provides a readily absorbed energy source. Lactose is the primary carbohydrate found in milk consisting of galactose and glucose. It requires lactase enzyme to digest. Maltose, made of two glucose units, is an intermediate product of starch breakdown. Trehalose has two glucose monomers linked in an atypical 1→1 bond, allowing it to provide stress protection [9]. Overall, the different disaccharides each serve specialized roles in nutrition, metabolism, and homeostasis. Further study of how disaccharide structures relate to their digestion, absorption, and utilization will provide insights to help optimize carbohydrate benefits.

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4. Oligosaccharide Structure and Function

Oligosaccharides are carbohydrate polymers containing between three to ten monosaccharide units. They can be linear or branched chains with a variety of glycosidic linkages. Oligosaccharides have many structural forms and are abundant on cell surfaces as components of glycoproteins and glycolipids where they facilitate molecular recognition and cell signaling [10]. Key dietary oligosaccharides include raffinose, stachyose, and fructooligosaccharides (FOS). Their structures and functions are outlined in Table 3.

Table 3: Structures and functions of common dietary oligosaccharides.

Oligosaccharide	Composition	Primary Functions
Raffinose	Galactose, glucose, fructose	Gas production, prebiotic
Stachyose	Galactose, glucose, fructose (2 units)	Gas production, prebiotic
FOS	Fructose polymers	Prebiotic, soluble fiber

Raffinose and stachyose contain galactose, glucose, and varying numbers of fructose units. They are indigestible oligosaccharides that provide prebiotic and gas-producing effects. Fructooligosaccharides (FOS) are short polymers of fructose that also display prebiotic activities. Overall, the structural diversity of oligosaccharides allows them to interact with gut microbes and gut epithelia in ways that modulate health [11]. Additional oligosaccharide research is needed to determine how best to leverage their structures for improved nutrition and disease prevention.

5. POLYSACCHARIDE STRUCTURE AND FUNCTION

Polysaccharides contain long chains of monosaccharide units linked together by glycosidic bonds. They are the most abundant carbohydrate class representing the primary storage and structural forms of carbohydrates. Plant polysaccharides include starch and cellulose, while animal polysaccharides include glycogen and chitin. The monosaccharide composition, chain length, branching structure, and glycosidic linkages influence the physical properties and functions of each polysaccharide (See Table 4).

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Table 4: Structures and functions of key dietary polysaccharides.

Polysaccharide	Composition	Primary Functions
Starch	α-D-glucose , α-1,4 linear with α-1,6 branches	Energy storage in plants
Cellulose	β-D-glucose , β-1,4 linear	Structural fiber in plants
Glycogen	α-D-glucose , α-1,4 linear with α-1,6 branches	Energy storage in animals
Chitin	β-D-N-acetylglucosamine , β-1,4 linear	Structural fiber in fungi, insects

Starch and glycogen are highly branched glucose polymers that serve as compact energy stores in plants and animals, respectively. Cellulose is an unbranched glucose chain that provides structural rigidity to plant cell walls. Chitin is an unbranched N-acetylglucosamine polymer that forms exoskeletons of insects and cell walls of fungi. These examples demonstrate how polysaccharides are structurally optimized for key biological roles. Further insights into polysaccharide conformations will lead to better use of dietary fibers and improved utilization of carbohydrate energy reserves.

6. Carbohydrate Digestion and Absorption

In order to utilize ingested carbohydrates, the digestive system must first break down polysaccharides into their monosaccharide constituents. Digestion begins in the mouth with salivary amylase which hydrolyzes some starch into maltose and dextrin disaccharides [12]. The bulk of carbohydrate digestion then occurs in the small intestine aided by pancreatic enzymes that further break down polysaccharides into oligosaccharides and disaccharides for absorption.

Intestinal cells lining the small intestine, called enterocytes, complete carbohydrate digestion through intracellular hydrolysis. Enterocytes express various membrane-bound disaccharidases and cytosolic glycosidases that split disaccharides, oligosaccharides, and any remaining polysaccharides into monosaccharides [13]. The monosaccharides glucose,

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galactose, and fructose are then absorbed across the intestinal epithelium into circulation via facilitated transport. Once absorbed, monosaccharides enter circulation and travel to tissues for utilization.

The efficiency of carbohydrate digestion and absorption depends heavily on molecular structure. For example, the glycosidic bonds of starch amylose and amylopectin differ in position and branching, leading amylopectin to be more readily digested. Fiber polysaccharides like cellulose are resistant to hydrolysis which prevents their breakdown and absorption [14]. Disaccharides also require their specific disaccharidases in order to be digested (See Table 5). Lactose cannot be absorbed without intestinal lactase to cleave it. These examples illustrate the critical impact carbohydrate molecular structure has on determining its fate and physiological effects during and after digestion.

Table 5: Digestive enzymes involved in carbohydrate breakdown.

Enzyme	Production Site	Substrate	Products
Salivary amylase	Salivary glands	Starch(amylose, amylopectin)	Maltose, dextrin
Pancreatic α-amylase	Pancreas	Starch, glycogen	Maltose, dextrin
Oligo-1,6-glucosidase	Small intestine	Oligosaccharides	Glucose
Sucrase	Small intestine	Sucrose	Glucose, fructose
Maltase	Small intestine	Maltose	Glucose
Lactase	Small intestine	Lactose	Glucose, galactose

7. CARBOHYDRATE ENERGY METABOLISM

Following digestion and absorption, carbohydrates undergo cellular metabolism to produce energy. The monosaccharides glucose and fructose enter glycolysis, a cytoplasmic

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pathway that breaks down 6-carbon sugars into two 3-carbonglycolytic intermediates called pyruvate. Glycolysis yields a net gain of two ATP molecules and two NADH coenzymes. Pyruvate can then enter the mitochondria where it is completely oxidized by the tricarboxylic acid (TCA) cycle producing additional energy equivalents and substrates for cellular respiration [15].

Glucose serves as the primary input for glycolysis in most cells. Phosphorylation traps glucose inside the cell. Hexokinase then converts glucose to glucose-6-phosphate, committing it to further catabolism. The intermediates of glycolysis include three-carbon sugars such as glyceraldehyde 3-phosphate and dihydroxyacetone phosphate as well as the phosphoesters 2,3-bisphosphoglycerate and phosphoenolpyruvate. Multiple isozyme forms of glycolytic enzymes exist with differences in kinetic parameters, allosteric regulation, and tissue distribution reflecting the varied metabolic needs of cells [16].

All aerobic organisms completely oxidize glucose for maximum energy yield. Under anaerobic conditions, glycolysis allows net ATP production through substrate level phosphorylation alone. This makes glycolysis a fundamental pathway conserved across species. However, glycolysis is regulated differently in various tissues to match carbohydrate utilization to energetic and biosynthetic demands. For example, liver uptakes and metabolizes glucose as needed whereas brain glycolysis is constantly active to provide its high glucose requirement [17].

Besides glucose, galactose and fructose also feed into glycolysis after initial processing steps. Galactose is converted to glucose-6-phosphate by the Leloir pathway in the liver and then metabolized like glucose [18]. Fructose enters its eponymous pathway involving phosphorylation by fructokinase and cleavage by aldolase B ultimately generating glycolytic intermediates. However, fructose metabolism bypasses key regulatory steps leading to unrestrained production of substrates that drive lipogenesis [19]. This provides a molecular mechanism for the association between excess fructose consumption and adverse metabolic effects.

Overall, the glycolytic pathway exemplifies how carbohydrate structure relates to function. The distinct fates of glucose versus fructose during metabolism combined with tissue-specific control of glycolysis allows this conserved catabolic route to support diverse physiological needs. Additional insights into carbohydrate structures and fluxes through

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intersecting metabolic pathways will further unveil the complexities of systemic energy homeostasis relevant to health and disease.

8. GLYCOPROTEIN SYNTHESIS AND FUNCTION

In addition to energy metabolism, carbohydrates play a crucial role in protein glycosylation. Glycoproteins contain one or more covalently attached glycan chains that affect protein folding, distribution, stability, and activity. Glycans contribute to protein structure while also serving as vital cell surface recognition elements mediating cell-cell and cell-matrix interactions [20].

Glycoprotein glycans are assembled in a step-wise manner from monosaccharide building blocks. The most prevalent sugars incorporated are glucose, mannose, galactose, fucose, N-acetylglucosamine and N-acetylneuraminic acid which comprise over 90% of all mammalian glycan structures [21]. Hundreds of glycosyltransferase enzymes catalyze the formation of glycosidic linkages to extend glycans via the various sugar monomers. Branch points and chain termination are mediated by glycosidases. This enzymatic balance determines the ultimate glycan structures attached to proteins [22].

The particular glycan configurations synthesized create distinct binding epitopes for lectins and other carbohydrate-binding proteins that induce downstream signaling effects [23]. For example, glycans attached to cell surface receptors can alter ligand binding and activation. Changes in glycan structures are associated with cancer, autoimmunity, and congenital disorders of glycosylation highlighting the essential contributions of glycans to protein activities [24]. Therapeutics targeting glycan biosynthesis pathways continue to be explored for modulating protein functions in disease contexts [25].

In summary, the step-wise synthesis of glycoprotein glycans from carbohydrate substrates coupled with their subsequent recognition by binding partners represents a fundamental form of post-translational modification regulating protein structure and function. Continued efforts to elucidate glycan assembly pathways and decode glycan structural motifs will further unlock the secrets of this complex carbohydrate signaling system.

9. CARBOHYDRATES IN CELL SIGNALING

Beyond protein glycosylation, carbohydrates participate directly in cellular communication systems as well. They can form ligands that bind cell surface receptors to

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trigger signaling cascades that alter cell behavior and physiology. Key examples include glycan-binding receptors of the C-type lectin family and glycosphingolipid signaling [26].

C-type lectins include selectins, collectins, and other receptors that bind carbohydrate chains in a calcium-dependent manner. Selectins facilitate cell adhesion and migration during inflammation and wound repair by interacting with sialylated and fucosylated glycans [27]. Collectins are soluble lectins that recognize glycan pathogen-associated molecular patterns (PAMPs) as part of the innate immune response [28]. Changes in carbohydrate structures provoked by inflammatory stimuli, hormones, or disease processes can dynamically alter lectin activities.

Glycosphingolipids contain carbohydrate head groups attached to a ceramide lipid backbone embedded in cell membranes. As both glycans and lipids transduce signals, glycosphingolipids integrate these pathways eliciting downstream effects on growth, differentiation, and motility through direct receptor binding or membrane domain organization [29]. Gangliosides are sialic acid-containing glycosphingolipids abundant in neuronal membranes where they modulate ion channel activities [30]. Defects in ganglioside catabolism lead to GM1 and GM2 gangliosidoses characterized by severe neurological impairment.

Together these examples demonstrate that carbohydrates directly participate in cell-cell communication mechanisms beyond their roles as passive protein modifiers. Specific carbohydrate motifs interact with various glycan-binding proteins and lipids to initiate signaling cascules that dynamically regulate cell functions. Further research into glycomic and glycobiological mechanisms will continue elucidating the diverse signaling roles of carbohydrates.

10. CARBOHYDRATES IN HEALTH AND DISEASE

Given the widespread involvement of carbohydrates in human physiology, it follows that aberrations in carbohydrate metabolism provoke development of disease. Changes in carbohydrate structures, concentrations, and fluxes through metabolic pathways have all been associated with pathology [31]. One of the most prevalent diseases linked to carbohydrate dysregulation is diabetes mellitus which is characterized by hyperglycemia arising from defects in insulin secretion, insulin action, or both [32].

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Chronic hyperglycemia leads totissue damage through increased protein glycation and generation of reactive oxygen species. Major complications of diabetes include retinopathy, nephropathy, neuropathy, and cardiovascular disease which all involve biomolecular damage from elevated blood glucose [33]. Strict control of carbohydrate intake and metabolism through insulin therapy, other drugs, diet, and exercise provides the cornerstone of diabetes management to prevent long-term sequelae.

Beyond diabetes, alterations in specific carbohydrate structures have been implicated in congenital disorders, cancer, autoimmunity, and susceptibility to pathogens. For example, defects in N-glycan synthesis pathways underlie congenital disorders of glycosylation associated with severe developmental impairment [34]. Thedensity of cell surface glycan branching is increased in tumorigenic cells which may impact metastasis [35]. Antibodies against glycoprotein glycans and glycolipids attack self-tissues in Guillain-Barre syndrome and other autoimmune neuropathies [36]. Viral and bacterial lectins that bind cell surface glycans facilitate infection highlighting the pivotal roles carbohydrates play on both sides of host-pathogen interactions [37].

In summary, precise regulation of carbohydrate chemistry is required to maintain normal physiology. Perturbations in carbohydrate structures, metabolism, or signaling contribute broadly to the pathogenesis of diverse diseases. Continued efforts to define carbohydrate involvement in disease processes may reveal novel glycan biomarkers and therapeutic targets to improve prevention and treatment.

11. CURRENT TRENDS AND FUTURE DIRECTIONS

Carbohydrate research remains an active field as the critical importance of glycobiology in human health becomes increasingly apparent. Major research directions include:

- Development of improved analytical methods for characterizing carbohydrate structures. Advances in mass spectrometry and NMR enable detailed compositional and conformational analysis of glycans to define structure-function relationships [38].
- Mapping of glycan biosynthesis pathways. Genomic, transcriptomic, proteomic, and metabolomic approaches are combining to identify glycosyltransferases, glycosidases, substrates, products, and regulators to model cell-specific glycan assembly [39].

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- Investigation of glycan recognition and signaling. Glycan arrays, glycan binding assays, and co-crystal structures precisely define lectin-glycan interactions while improving understanding of downstream signaling effects [40].
- Engineering of synthetic glycans and glycomimetics. Chemical and enzymatic glycan synthesis allows generation of homogeneous glycan probes to study and modulate glycan activities in vivo [41].
- Integration of glycomic data into systems biology models. Databases of glycan structures and biosynthetic pathways support systems-level modeling of glycan functions in metabolism, signaling, and overall network dynamics [42].
- Development of glycan-based biomarkers and therapeutics. Aberrant glycans show promise as early disease indicators while glycan biosynthetic enzymes are emerging drug targets [43].

Overall, recent technological and bioinformatic advances have propelled the glycosciences forward into the post-genomic era. The coming decades will continue to see major discoveries related to fundamental glycan biology that translate into clinical tools for managing carbohydrate-related diseases. These future glycomic applications will firmly establish carbohydrates as essential biomolecules crucial for supporting human life and health.

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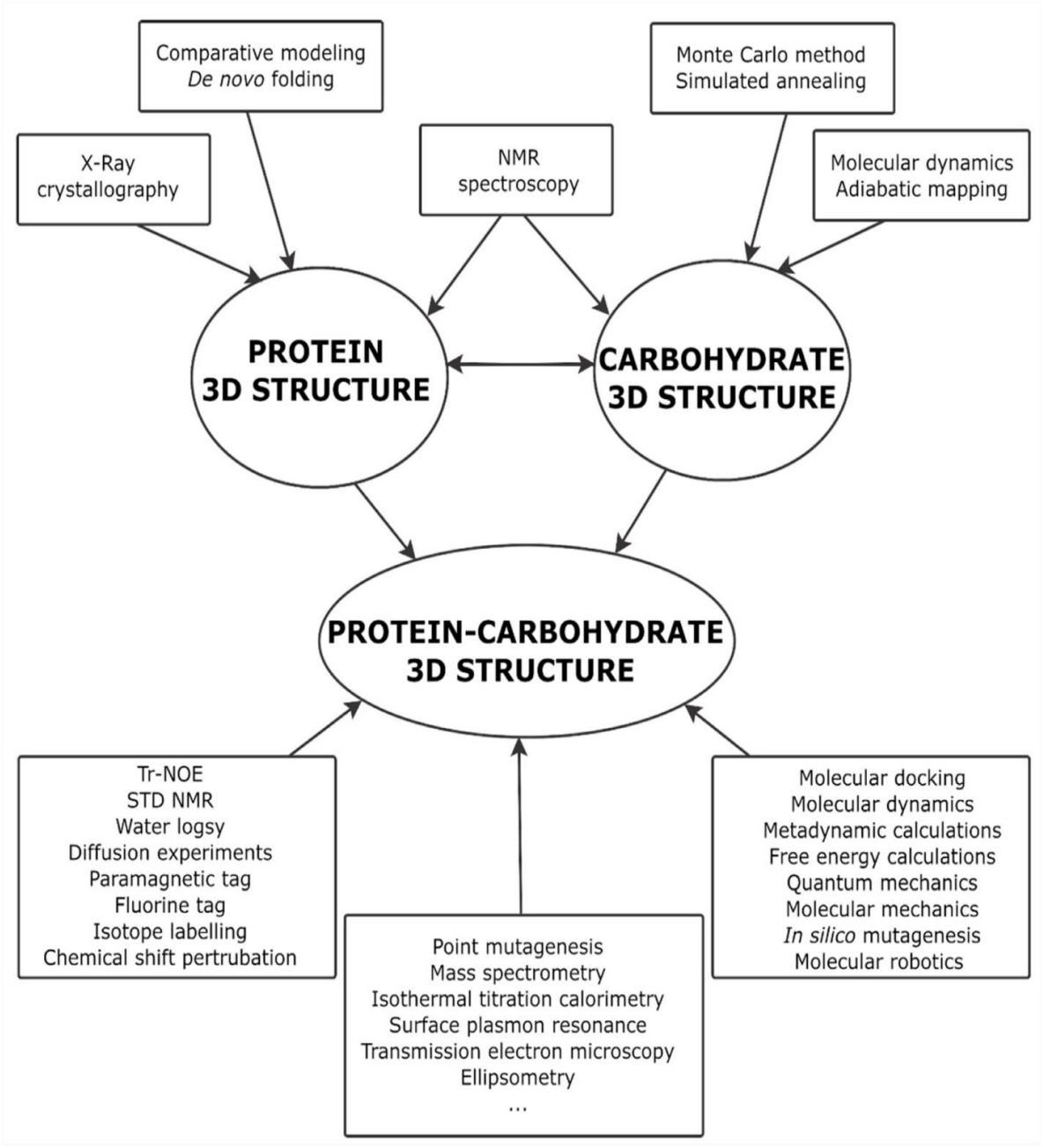

Figure 2: Interplay of the instrumental and computational methods in the 3D structure determination of carbohydrates, proteins, and protein–glycoconjugate complexes

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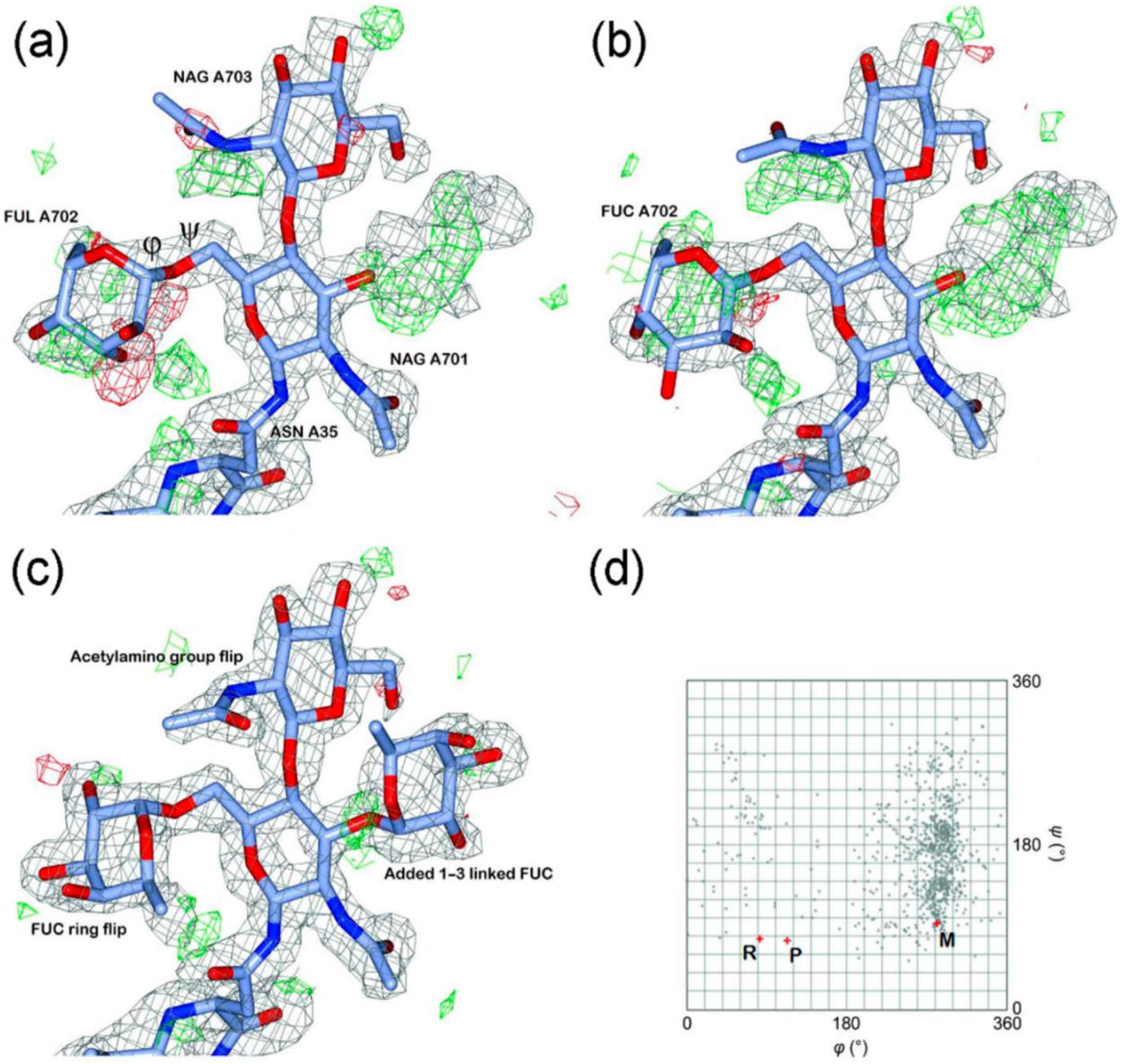

Figure 3 (a) Original glycan structure model from the PDB entry. 3(b) PDB-REDO model with properly renamed fucose residue and improved fit to the electron density. 3(c) Manually rebuilt model based on PDB-REDO results. 3(d) CARP distribution plot for glycosidic φ-ψ torsions of FUC(1-6)NAG (from panel (a)) in PDB.

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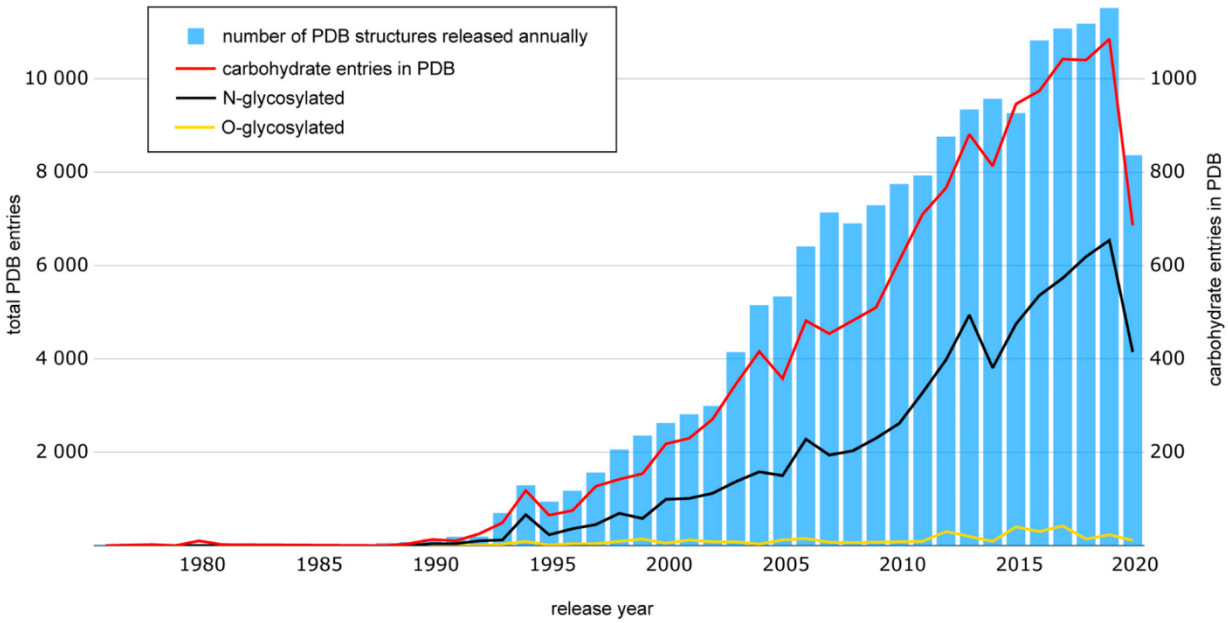

Figure 4: Deposition statistics of carbohydrate-containing structures in Protein Data Bank based on carbohydrate remediated list data. Data for 2020 cover seven of twelve months

12. CONCLUSION

In conclusion, this broad review integrates principles from carbohydrate chemistry, biochemistry, physiology, and pathology to provide a structural perspective on the diverse functional roles of carbohydrates in biological systems. Key topics covered include:

- Carbohydrate classification, nomenclature, and molecular structures
- Monosaccharide, disaccharide, oligosaccharide, and polysaccharide configurations in relation to their biological activities
- Carbohydrate digestion, absorption, and intracellular metabolism
- Glycoprotein synthesis and function
- Roles of carbohydrates in cell-cell signaling mechanisms
- Involvement of carbohydrates in health and disease processes
- Current trends and future research directions in the glycosciences

The form-function relationships of carbohydrate structures give rise to their widespread capabilities as energy sources, metabolic intermediates, stable polymers, dynamic post-translational modifiers, cell surface ligands, and more. Appreciation of these structure-

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activity correlations is critical for improving carbohydrate utilization and developing glycan-targeted therapeutics. This overview of carbohydrate chemistry and biology provides a foundation for ongoing research efforts seeking to fully elucidate the diverse molecular roles of these essential biomolecules.

13. CONFLICT OF INTEREST

The authors declared no potential conflicts of interest with respect to the research, authorship, and/or publication of this article**.**

14. PLAGIARISM POLICY

All authors declare that any kind of violation of plagiarism, copyright and ethical matters will taken care by all authors. Journal and editors are not liable for aforesaid matters.

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