



Enantiomers of Carbohydrates and Their Role in Ecosystem Interactions: A Review

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Received: 6 February 2020; Accepted: 12 March 2020; Published: 17 March 2020



Abstract: D- and most L-enantiomers of carbohydrates and carbohydrate-containing compounds occur naturally in plants and other organisms. These enantiomers play many important roles in plants including building up biomass, defense against pathogens, herbivory, abiotic stress, and plant nutrition. Carbohydrate enantiomers are also precursors of many plant compounds that significantly contribute to plant aroma. Microorganisms, insects, and other animals utilize both types of carbohydrate enantiomers, but their biomass and excrements are dominated by D-enantiomers. The aim of this work was to review the current knowledge about carbohydrate enantiomers in ecosystems with respect to both their metabolism in plants and occurrence in soils, and to identify critical knowledge gaps and directions for future research. Knowledge about the significance of D- versus L-enantiomers of carbohydrate metabolism in plants with respect to pathogen and pest control and ecosystem interactions represent the knowledge gaps and a direction for future research.

Keywords: carbohydrate enantiomers; plant metabolism; soil microorganisms; transgenic plants; pests and pathogens; cellulose; hemicelluloses; and lignin

1. Introduction

Carbohydrates play a central role in cell metabolism and are a primary product of photosynthesis. They belong to the most abundant organic compounds of terrestrial ecosystems and are used in chemical research [1–3]. Carbohydrates enter the ecosystems by means of dry deposition, rainfall, throughfall, and especially through stemflow [4,5]. Leaching of carbohydrates from vegetation is of significance in sites loaded by acid deposition. Neutral sugars have been identified and analyzed in aerosols at urban and forested suburban sites, where glucose and mannose were found to be dominant [6]. Carbohydrates are precursors for the synthesis of many biochemically active compounds and are important in terms of interactions between organisms of different trophic levels, having

great significance for plant nutrition and phytoremediation [7]. Glucose, xylose, arabinose, galactose, rhamnose, and uronic acids represent the dominant carbohydrates of plant and animal tissues (Table 1).

Plant/Animal	Type of Material	Dominant Carbohydrate	References
Acacia sp.	Water-extract	Galactose	[8]
Algea	Exopolysaccharides	Glucose, arabinose, mannose, rhamnose, galactose and xylose	[9]
Aromatic plants	Leaves	Glucose, fructose	[10]
Banana plants	Petioles	Arabinose, galactose, glucose	[11]
Beech, Oak	Litter	Xylose, glucose, galactose, arabinose	[12]
<i>Canavalia</i> sp.	Fiber	Uronic acid, glucose, arabinose	[13]
Cannamonum sp.	Extracted polysaccharide	Mannose, galactosamine	[14]
Chorisia speciosa	Seed coat	Galactose	[15]
Cochlospermum gossipium	Gum	Uronic acid	[16]
Cordia abyssinica	Fruits	Galactose, rhamnose	[17]
Corn	Litter	Xylose, glucose	[18]
Cryptomeria japonica	Xylem	Glucose, galactose, xylose and fucose	[19]
Different plants	Gums	Arabinose, galactose	[20]
-	Seed mucilage	Maltose	
<i>Eucalyptus</i> sp.	Wood	Glucose	[21]
Grassland community	Leaves	Arabinose, xylose, mannose, arabinose and glucose	[22]
Transgenic plants	Cell walls	Glucose, xylose	[23]

Table 1. Dominant carbohydrates of plants.

The ability of carbon atoms to form chiral structure is the basis of living systems on the Earth [24]. In several studies, chirality has been considered in terms of a branching index [25,26]. L- and D-enantiomers of carbohydrates occur naturally and have different roles in different organisms: L-mannose and L-rhamnose, bacterial polysaccharides and mucilages (gellan, welan, rhamsan); L-arabinose such as plant gums and bacterial polysaccharides; D-arabinose, aloe glycosides; D-rhamnose, a capsid of Gram-negative bacteria; D-fucose, cardiac glycosides and resins of trees; and L-fucose in blood group substances [27]. Sharp decline in soil nutrient (carbohydrate, soil carbon and soil nitrogen) across ecotone is also reported in some research [28,29]. The present review paper summarizes the knowledge on enantiomers of carbohydrates in terrestrial ecosystems, their role in ecosystem interactions, and highlights important areas for future research.

2. D- and L-Carbohydrates of Plants

Cellulose, hemicelluloses, and lignin represent the major biochemical components of plants [30]. Carbohydrates form up to 93% of plant dry weight and have many roles in plants including building up biomass and carbon storage, being the precursor for the synthesis of many compounds including glycosides, saponins, glycoproteins, and acting as defense compounds against pathogens, herbivory, and abiotic stress [31–36].

2.1. Role of Carbohydrates under Stress and Protection against Herbivory

Osmolytes including carbohydrate are other neutral molecules that protect plants under various stress factors [37]. These metabolites include proline, sucrose, polyols, and trehalose (Figure 1), and they protect the plant under stress conditions by conserving the cellular function of plant. Many reports have suggested the role of osmolytes in drought [38], predator, and pesticide stress [39–41] Figure 2 represents the structure of some osmolytes. Accumulation of myo-inositol indicates membrane disintegration due to air pollution [42]. Pectic polysaccharide mucilage plays an important role in plant tolerance to salinity stress when it increases in stems, shoots, and roots with increased uronic acid and rhamnose [43]. Furthermore, flavonoid and chitinase gene expression are plant defense mechanism

responses to insect herbivory [35]. Cyanogenic glycosides, a secondary metabolite of the plant, is composed of alpha-hydroxy nitrile and D-glucose moiety; these compounds are potentially dangerous to animals and humans due to the presence of hydrogen cyanide (HCN). Release of such substances occurs spontaneously or through enzymatic regulation by the plant.



Figure 1. Schematic representation of the plant's response to various abiotic stresses and the role of osmolytes under stressful conditions [44].



Figure 2. Structure of some carbohydrate origin osmolytes present in plants.

Cassava roots, rich in starch, acting as goitrogens (substances that disrupt the production of thyroid hormones by interfering with iodine uptake in the thyroid gland) [45]. The lectins (carbohydrates

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containing glycoproteins) of some plants (*Croton triglium, Abrus precatorius, Robinia pseudoacacia*) are toxic to humans and animals, leading to loss of appetite, decreased body weight, and death [46]. Soybean saponins protect plants from *Callosobruchus chinensis*, whereas higher animals are able to degrade these compounds [47]. Saponins exert a strong activity on lepidopteran cells, presumably based on a cytotoxic action due to permeation of the cell membrane [48]. Latex proteins of mulberry-silkworms inactivate chitinase and protect plants from insect herbivory [34]. Lecitin glycoproteins (3% of carbohydrates) from *Arisaema* sp. have insecticidal properties [49]. Some plant β -glycosides (phlorizin, amygdalin or prunasin) inhibit trehalase, a key enzyme of glucose metabolism in insects [50].

Plant chlorogenic acid is an inhibitor of glucose-6-phosphate translocase [31]; it increases with nematode attack and other types of stress [51]. Furthermore, abiotic stress increases galactose and raffinose levels in the plants [36]. The significant role of carbohydrates like pinitol, ononitol, mannitol, and inositol has been proven in plant defense against Erwinia amylovora [52]. Increased expression of β -1,3 glucanases in flax increases resistance to fungi [53]. On the other hand, fructose of exuded tree sap was found to stimulate the growth of all tested saprophagous butterflies, whereas the glucose feeding stimulatory effect was found only for some [51]. The galactinol synthase (which occurs in three isoforms) gene (CaGolS1-2-3), which catalysis the raffinose family of carbohydrates in plants, is upregulated by abiotic stress [54]; the gene has been cloned [55].

The above findings summarize that abiotic and biotic stress factors alter the carbohydrate metabolism of plants. However, the mechanisms of the alterations are not fully understood [56]. Carbohydrates have cryoprotective and osmoregulatory properties they accumulate under salt stress or pathogen attack (sucrose, pinitol), or act as reactive oxygen species scavengers including contribution to membrane stabilization via reaction with phospholipid headgroups (as reported for raffinose) increasing chilling tolerance [34]. On the other hand, pollutants such as Ozone, Sulfur dioxide, and Nitrogen Oxides are hypothesized to cause de-esterification of membrane lipids, leading to increased concentrations of free carbohydrates such as myo-inositol [43]. Only a few plant proteins are known to inactivate enzymes of the carbohydrate metabolism of some insects, and more research is necessary to understand the mechanism and adaptation of plant defense against herbivory [34].

2.2. Occurrence Of D- and L-Carbohydrates, Their Metabolism in Plants, and Its Genetic Regulation

The plant contains several Levo form of carbohydrates like L-arabinose, L-fucose, L-rhamnose, and L-galactose. The carbohydrate content of the plant is not fixed and changes from season to season [57]. Most plant carbohydrates are generated by the sequential conversion of UDP-D-glucose, whereas L-fucose and L-galactose in plants are derived from GDP-D-mannose. L-fucose formation requires the presence of enzyme GDP-D-mannose-4,6-dehydratase (GMD) and GDP-4-keto-6-deoxy-dmannose-3,5-epimerase-4-reductase (GER), whereas, on the other hand, GDP-L-galactose is formed by the GDP-D-mannose 3,5-epimerase (GME) enzyme [58,59]. Plants synthesize UDP-sugar by an enzyme encoded by gene RHM that leads to the conversion of UDP-D-glucose into UDP-L-rhamnose [58]. UDP-D-glucose can be directly converted into UDP-D-galactose, UDP-D-glucuronic acid, or UDP-L-rhamnose. GDP-D-mannose can be converted into GDP-L-fucose by the action of enzyme GDP-D-mannose-4,6-dehydratase, or it can also be converted into GDP-L-galactose and GDP-L-glucose by enzyme GDP-D-mannose 3,5-epimerase. Pyrophosphatases and phosphatase enzymes catalyze the formation of either L-glucose or from UDP-L-glucose form UDP-L-galactose [59].

L-galactose is the starting material of ascorbic acid L-synthesis. N-methyl cyclopropane acts as an inhibitor of ascorbate synthesis from L-galactose [60]. Conversion of D-mannose to L-galactose is a limiting step of L-ascorbic acid synthesis. UDP-xylose is produced via catalysis by UDP-glucuronate decarboxylase [61]. The formation of xylans is accompanied by cross-linkages with lignin via alpha-L-arabinofuranosyl residues [62]. Methyltransferase involved in the formation of 4-O-methylglucuronoxylan in pea epicotyl is stimulated by UDP-D-xylose and UDP-D-glucuronic acid [63]. UDP-glucose dehydrogenase converts UDP-glucose to UDP-glucuronic acid, a precursor of

many sugars. The enzyme is inhibited by UDP-xylose; a multifunctional carbohydrate L-myo-inositol is produced from D-glucose-6-P via L-myo-inositol-1-P [64].

The genes StUGE45 and StUGE51 encoding UDP-glucose-epimerases, which catalyze the conversion of UDP-glucose to UDP-galactose, were isolated from potato tubers [51]. The genes PpARF1 and PpARF/XYL, encoding alpha-L-arabinofuranosidase or alpha-L-arabinofuranosidase/ beta-D-xylosidase, respectively, were identified in peach [65]. L-rhamnose is a major constituent of the pectic polysaccharides of Arabidopsis cell walls and is synthesized by three enzymes including the rhamnose synthase, which is encoded by AtRHM1, AtRHM2/AtMUM4, and AtRHM3 [66]. Two Arabidopsis genes, At1g45130 and At3g52840, encode for beta-galactosidase isozymes. [66,67]. Apoplastic beta-xylosidase and beta-glucosidase of Arabidopsis are encoded by the same gene AtXYL1 [68].

Hemicelluloses contain D-xylose, L-arabinose, D-mannose, D-glucose, and D-galactose, and small amounts of L-rhamnose and L-fucose. The glucuronoxylans of hardwood contain a small amount of L-rhamnose, while the arabinoglucuronoxylan of non-woody (agricultural crops) contains L-arabinose when the linear B-(1,4)-D-xylopyranose backbone is linked by the α -(1,2) and α -(1,3) glycosidic bond with 4-O-methyl- α -D-glucopyranosyl uronic acid and α -L-arabinofuranosyl [69].

Glucuronoarabinoxylan is the most abundant hemicellulose of corn stover. Xyloglucans predominant in hemicelluloses of primary cell walls of grasses contain large amounts of D-glucose, D-xylose as well as L-arabinose and L-fucose [2]. Xyloglucans of bilberries (an important crop of northern Europe) contain D-xylose and galactose plus L-fucose, the building blocks contain galactose-xylose and fucose-galactose-xylose side chains with acetylated galactose [70]. Xyloglucans of gymnosperm walls have D-carbohydrates predominantly and are similar to eudicotyledons and monocotyledons in also containing L-arabinose [71]. Arabinoxylans, major hemicelluloses of cereal cell walls, show higher L-arabinose content than hardwood xylans [69]. The xylan content of different tree species may reach up to 20% of dry matter [72] when they consist of a backbone of β -1,4-linked D-xylose residues containing side groups such as L-arabinose, D-galactose, or D-(4-O-methyl)-glucuronic acid [73].

Plant pectin contains D-galacturonate with a small amount of L-arabinose, D-galactose, and L-rhamnose [74]. L-galactose is essential for L-ascorbic acid synthesis with L-glucose and L-galactonic acid as intermediates [75]. Plant glycoalkaloids, especially chaconine, solamargine, and solanine, contain L-rhamnose and L-galactose sugar [76], which forms a disaccharide, bis-α-L-rhamnopyranosyl-β-D-glucopyranose or α-L-rhamnopyranosyl-β-glucopyranosyl-β-Lgalactopyranose with β-D-glucose. Arabic gums (branched-chain, complex polysaccharides, either neutral or slightly acidic) contain L-arabinose and L-rhamnose in the form of α-L-arabinofuranosyl and α-L-rhamnopyranosyl [77].

The primary cell walls of lycophytes have a high concentration of 3-O-methyl-D-galactose [77] Both D- and L-galactose are synthesized from UDP-D-glucose (via UDP-galactose) when D-galactose is more abundant in plants. Separation of the enantiomeric forms showed the ratio of D-/L-galactose ranged from 7.3 to 70, in the lycophytes or spinach cells when D-galactose oxidase oxidizes the –CH2OH group of D- but not L-galactose [78,79].

L-galactose dehydrogenase is an important enzyme of phenolic compounds, tocopherol, and ascorbic acid synthesis in plants, and is the catalysis for the conversion of D-galactose to L-galactono-1,4-lactone [80].Galactose induces the gene for dammarenediol synthase CabAS of plants and accumulates due to some diseases such as huanglongbing of citrus plants [81]. Galactose is toxic to *Albizzia* sp. root explants and other tissues and induces the gene for flavonoid glucosyltransferase expression [66].

2.3. Perspectives for Future Research

An approach has been used to elucidate the role of nucleotide sugar interconverting enzymes for the regulation of cell wall synthesis, [58,61], but their expression, kinetic properties, and intracellular

localization or modification of cell wall pectic polysaccharides are still poorly understood [67,82]. Research on transgenic plants is also targeted to reduce the content of some types of carbohydrates. The use of endogenous gene expression was reported to reduce the carbohydrate content of some transgenic plants (potato) or decrease rhamnogalacturonan by ectopic expression of rhamnogalacturonan lyase from *Aspergillus* sp. [83].

Many works deal with the metabolism of carbohydrates and ascorbic acid in plants [60,64,65,75], but its regulation and multifunctional role of some carbohydrates (e.g., myo-inositol) are still poorly understood. Moreover, many genes of carbohydrate transporters were not identified including factors regulating their expression and localization. In particular, biosynthesis control and the interplay of enantiomeric forms or phosphorylative processes represent knowledge gaps of the genes encoding enzymes included in carbohydrate metabolism [64]; only part has been functionally characterized [67]. Better understanding the action of plant hydrolytic enzymes involved in carbohydrate metabolism gives promise for industrial applications including the paper industry, preparation of animal feed, fabrication of sugar beet syrup, etc. with the replacement of microbially-derived enzymes [64]. Additionally, some plant biopharmaceuticals are glycoproteins produced through Golgi N-glycosylation [84].

3. Significance of Enantiomers of Carbohydrates for Invertebrates and Vertebrates

Insects and other animals assimilate both L- and D-carbohydrates [85]. Carbohydrates represent a major contributor to all trophic categories of insects with no or only a low contribution from the degradation of lignin [7]. *Protophormia terraenovae* is commonly called the northern blowfly, blue-bottle fly, or blue-assed fly. It is distinguished by its deep blue coloration and large size. Carbohydrate enantiomers act differently on the salt receptors of *Protophormia terraenovae*; L-fucose has a stronger stimulatory effect than D-fucose [86,87]. Polysaccharides have taxonomic significance for parasitology including the evolutionary line of *Crithidia* sp. [88].

L-fucose as well as some D-carbohydrates inhibits agglutination of rabbit erythrocytes [89]; L-arabinose and D-galactose, D-maltose, D-psicose, D-xylose, neuraminyl lactose and neuraminyl-Nacetyl-lactosamine or 1,5-anhydro-D-glucitol and enzymes (e.g., β -galactosyltransferase or N-acetyl- α -D-glucosaminidase) occur in the urine [90]. The ratio of L/D carbohydrates serves as an indicator of human diseases (i.e., the ratio of D/L arabinitol in cerebrospinal fluids (range: 8.6–2.8) indicates Candida infections [91]. Absorption of L-glucose in human intestines is higher than L-galactose or L-mannose and D-mannitol [92].

4. L- and D-Carbohydrates in Soil

Information about soil carbohydrates including the effects of management practices was reviewed by Vranova et al. (2013) [93]. Little knowledge exists about the enantiomers of carbohydrates in soil, both L-and D-carbohydrates occur in composts and humic substances in a ratio of 0.07 to 0.13 (Table 2) [94]. Aside from plant and animal biomass, L-carbohydrates enter soils from different sources including medical colon-cleansing agents, which enter soil through urine and feces [95].

Plant/Organism	Material	L/D Carbohydrates	Dominant Carbohydrates	References
American larch	Arabinogalactans of wood	6	D-galactose, L-arabinose	[96]
Cochlospermum religiosum	Heteropolysaccharides from gum	1	L-rhamnose, D-galactose, D-galacturonic acid	[97]
Dalbergia sissoo	Acid polysaccharide	0.16	L-rhamnose, D-glucose, D-galactose	[98]
Human	Urine	0.13	D-glucose, L-fucose	[99,100]
Rat	Feces	0.5	D-galactose, L-fucose	[101]
Soil	Humic substances	0.13	D-glucose, L-fucose	[94]
Composts	-	0.07-0.09	D-glucose, L-fucose	[94]
Pseudotsuga menziesii	Bark holocellulose	0.04	L-arabinose, D-glucose	[102]

Table 2. Ratio of L- versus D-carbohydrates in different materials.

L-arabinose, L-rhamnose, and L-fucose are commonly included in soil respiration tests because these sources are found in substrates that are highly correlated with the metabolic diversity of the soil microbial community [103,104]. Plant species composition affects L-rhamnose utilization in the rhizosphere with the highest utilization rate for wheat [105]. Utilization of L-rhamnose is also significantly negatively correlated with microbial diversity of regenerated forest sites or rhizosphere [106]. Utilization of L-rhamnose (and D-galactose, m-inositol, D-psicose) by the rhizosphere soil microbial community decreases with plant age [107,108]. D-xylose is used as a biostimulator of the microbial consortium for the degradation of pollutants [109].

Decomposition of *Fraxinus excelsior* leaves increases the proportion of glucose to other monosaccharides [110] when soil α -glucosidase is slightly inhibited or activated by some L- and D-carbohydrates including L-arabinose and L-rhamnose, D-xylose, D-mannose or D-glucose [111]. Additionally, D-imino sugars and some amino acids such as 3- or 4-hydroxyproline are glycosidase inhibitors [112,113].

Overall, works published on carbohydrates and their microbial metabolism indicate that D- versus L-carbohydrates play different roles in soils. In particular, the inhibition/stimulation of soil enzymes (α -glucosidase, glycosidases) differ with respect to the type of carbohydrate enantiomers. Generally, L-carbohydrates are less inhibitory to α -glucosidases compared to D-enantiomers; especially with the addition of nutrients such as iron. Only L-carbohydrates increased α -glucosidase activity [114–119]; the mechanism of this effect is not known yet.

5. Conclusions

Understanding the metabolism of carbohydrates in plants, their genetic regulation, and their use as an indicator of stress, pollution, and pest control represents a target of future research. Other potential future research includes the elucidation of the upregulation mechanisms of genes that are involved in carbohydrate synthesis and the inhibition of key enzymes of biochemical pathways. The use of plant breeding to regulate glycoalkaloids and carbohydrate inputs to the soil via rhizodeposition represents a future way to improve plant nutrient acquisition that increases the efficiency of phytoremediation and reduces the emissions of greenhouse gases. Development of transgenic plants is targeted to regulate carbohydrates and synthesis of carbohydrate-containing compounds used in the food and pharmaceutical industries. There is also a knowledge gap concerning the occurrence and significance of L- versus D-enantiomers of carbohydrates and carbohydrate-containing compounds in soil organic matter that affect nutrient cycling (e.g., inhibition of phosphatase activity) and interactions between different organisms [120].

Future research requires a detailed understanding of plant defense mechanisms against herbivory and pathogens via gene expression of plant carbohydrate metabolism. The search continues for effective inhibitors of trehaloses of insects, molluscans, and fungi to control pests and other harmful organisms, and to understand the formation of plant glycosylated compounds that are of potential danger for animals and humans.

Author Contributions: Conceptualization, L.L. and M.B.; Methodology, P.F., I.D., and V.V.; Validation V.V. and I.D.; Formal analysis, R.D.; Resources, M.B.; Data curation, L.L.; Writing—original draft preparation, L.L.; Writing—review and editing, R.D.; Visualization, R.D. and MB.; Supervision, P.F. and I.D.; All authors have read and agreed to the published version of the manuscript.

Funding: This research received no external funding.

Acknowledgments: This text was prepared within the framework of grant RO0218 supported by the Ministry of Agriculture of the Czech Republic.

Conflicts of Interest: The authors declare no conflicts of interest.

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