



Review

Dextran: Sources, Structures, and Properties

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Abstract: Dextran is an exopolysaccharide (EPS) synthesized by lactic acid bacteria (LAB) or their enzymes in the presence of sucrose. Dextran is composed of a linear chain of D-glucoses linked by α -(1 \rightarrow 6) bonds, with possible branches of D-glucoses linked by α -(1 \rightarrow 4), α -(1 \rightarrow 3), or α -(1 \rightarrow 2) bonds, which can be low (<40 kDa) or high molecular weight (>40 kDa). The characteristics of dextran in terms of molecular weight and branches depend on the producing strain, so there is a great variety in its properties. Dextran has commercial interest because its solubility, viscosity, and thermal and rheological properties allow it to be used in food, pharmaceutical, and research areas. The aim of this review article is to compile the latest research (in the past decade) using LAB to synthesize high or low molecular weight dextran. In addition, studies using modified enzymes to produce dextran with specific structural characteristics (molecular weights and branches) are addressed. On the other hand, special attention is paid to LAB extracted from unconventional sources to expose their capacities as dextran producers and their possible application to compete with the only commercial strain (*Leuconostoc mesenteroides* NRRL B512).

Keywords: lactic acid bacteria; exopolysaccharides; dextran; structure; properties



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1. Introduction

Lactic acid bacteria (LAB) are microorganisms that produce lactic acid as the main or only product of carbohydrate fermentation (heterofermentation or homofermentation, respectively). The nutritional requirements are complex, since they are based on vitamins, minerals, fatty acids, amino acids, peptides, and carbohydrates, which are usually in their natural habitats [1]. LAB have been isolated from dairy foods, meats, cereals, vegetables, soil, water, and vaginal waste. According to their characteristics and taxonomy, LAB include bacteria belonging to the genera *Aerococcus*, *Alloiooccus*, *Carnobacterium*, *Dolosigranulum*, *Enterococcus*, *Globicatella*, *Lactococcus*, *Lactobacillus*, *Leuconostoc*, *Oenococcus*, *Pediococcus*, *Streptococcus*, *Vaiscoccus*, and *Weiscoccus* [2]. LAB are considered probiotic bacteria because they can be incorporated into food to improve the consumer's intestinal microbial balance, and they are also generally recognized as safe (GRAS) because they are not pathogenic for humans [3]. On the other hand, they are responsible for a great diversification of flavors and textures of food products, which is why they are mainly used to produce different fermented products such as yogurt, cheese, sourdoughs, pickles, sausages, and soy products [4]. In addition, some LAB can produce extracellular polysaccharides (called exopolysaccharides, EPS) that are repeat units of sugars such as glucose, galactose, and rhamnose, which are secreted during bacterial growth [5]. EPS can be classified into two groups depending on the units that comprise it. Heteropolysaccharides consist of different monosaccharide units, for example, xanthan and gellan. Homopolysaccharides are composed of repeating units of a single type of monosaccharides (e.g., glucose or fructose), for example, glucans and fructans. Levan and inulin are the fructans produced by LAB, while the most commonly produced glucans are cellulose, pullulan, curdlan, mutan, alternan, and dextran [6]. These natural polysaccharides have been used as carriers, encapsulants, thickeners, binders, lubricants, and additives in the pharmaceutical and food industries [7]. However, the most important EPS for medical and industrial use is

dextran, which was initially believed to be synthesized only by *Leuconostoc mesenteroides*, but subsequent research reported its segregation by another type of LAB (see Section 2) [8]. The literature on the identification or characterization of dextrans produced by LAB has been increasing in the past decade, as can be seen in Figure 1. Therefore, the aim of this review is to show the advances that have been made in the discovery and characterization of new dextrans, their structural characteristics (molecular weight, links, and branches), and a brief description of their possible applications in medical, food, and research areas. In addition, emphasis is placed on extraction sources for dextran-producing bacterial strains.

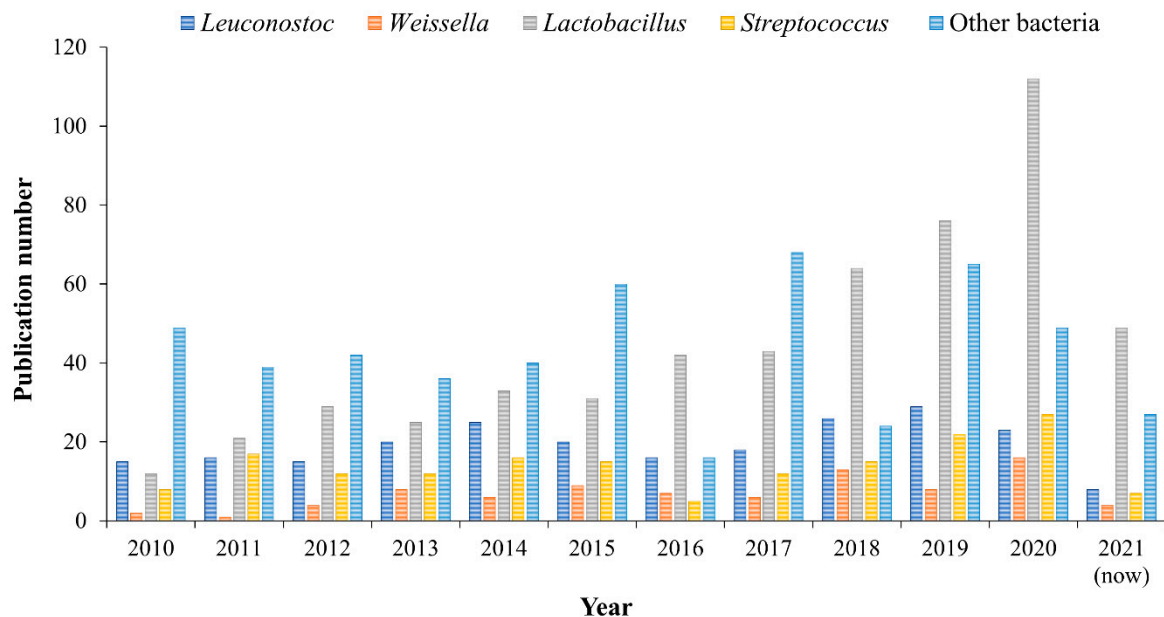


Figure 1. Number of publications related to dextran synthesis by lactic acid bacteria (source: Scopus; keywords: Bacteria, *Leuconostoc*, *Weissella*, *Lactobacillus*, and *Streptococcus*; accessed: 3 May 2021).

2. Synthesis of Dextran

Dextran is synthesized in a particular way by LAB when exposed to a medium with sucrose as a carbon source [8]. In some LAB (e.g., *Lactobacillus*), sucrose can enter the cell directly via the phosphotransferase system (PTS) and metabolize to form D-lactate or become dextran [9]. Bacterial dextransucrases, located extracellularly, are responsible for hydrolyzing sucrose in its fructose and glucose monomers, forming an intermediate with glucose (glycosyl-enzyme) to later carry out their polymerization and form dextran [10], while the resulting fructose enters the bacteria through PTS to meet its metabolic demand [11], as shown in Figure 2. LAB that report dextran production are mainly of the genus *Leuconostoc*, *Weissella*, *Lactobacillus*, and *Streptococcus* [10], which have been isolated from different plant sources (e.g., *Agave salmiana* and pummelo) [12,13] and fermented products (e.g., rice batter, cabbage, idli batter, and pickles) [14–17]. However, dextran can also be synthesized via enzymatic, directly using dextransucrases (sucrose: 1,6- α -D-glucan 6- α -D-glucosyltransferase, EC 2.4.1.5) [18], which polymerize the glucoses of the sucrose in dextran, as shown at the top of Figure 2.

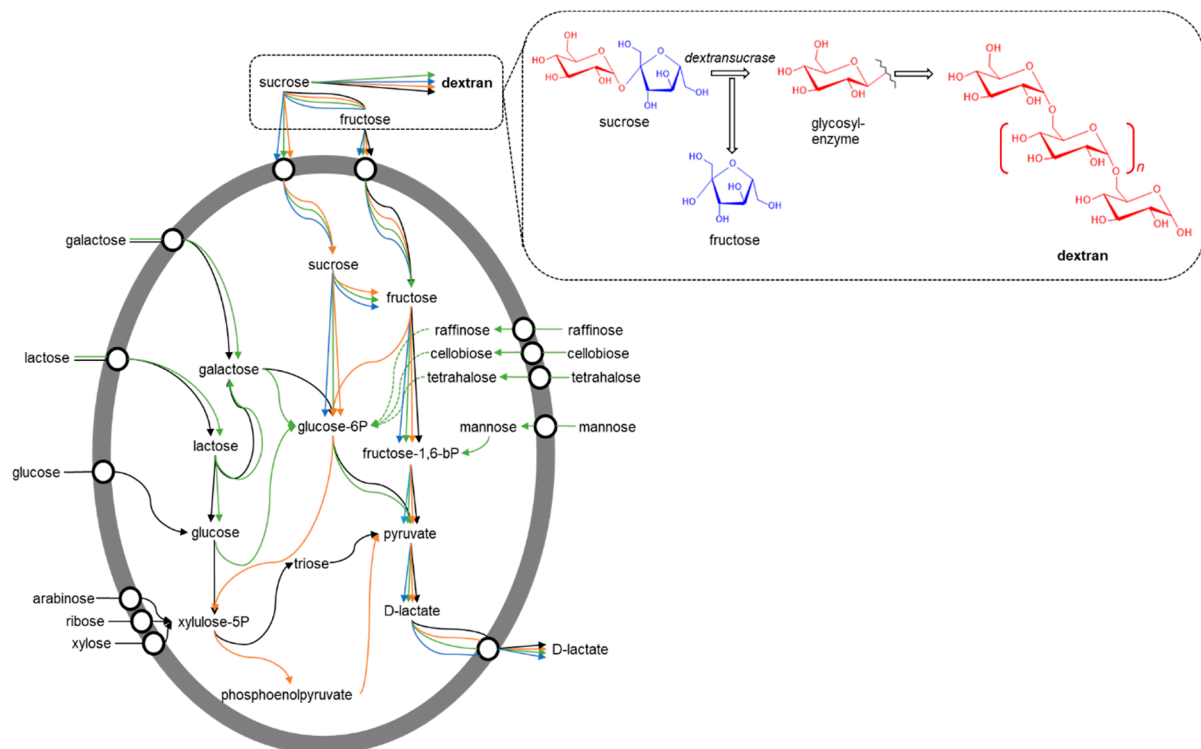


Figure 2. General carbohydrate pathways and dextran synthesis in lactic acid bacteria: *Leuconostoc* (black), *Weissella* (orange), *Lactobacillus* (blue), and *Streptococcus* (green). Adapted from [9–11,19,20].

In industry, dextran is obtained through the culture of *Leuconostoc mesenteroides* NRRL B512, because it is considered a bacteria generally recognized as safe (GRAS) and very stable [21]. The fermentation of the NRRL B512 strain is carried out in a sucrose medium, which is nourished with yeast extracts, malt extracts, casein, peptone, and tryptone; in addition, low levels of calcium and phosphate are added [22–25]. During fermentation, the pH drops from 7 to 5 due to the generation of lactic acid; therefore, non-ionic detergents are usually added to maintain the stability of the bacteria and its enzymes [8]. In the clinical area, dextran is usually obtained from the acid hydrolysis (e.g., sulfuric and hydrochloric acids) of the native dextran from *Leuconostoc mesenteroides* NRRL B512, which allows controlling the molecular weights of the resulting dextrans [26,27].

3. Characteristics of Dextran

Dextran is a complex glucan formed by a main chain of D-glucoses linked by α -(1→6) bonds with possible branches of D-glucoses with α -(1→4), α -(1→3), or α -(1→2) bonds [28], as shown in Figure 3. Dextrans have molecular weight of up to 440 MDa [29], and they can be classified into two types according to the length of their chains—those with molecular weight greater than 40 kDa are simply called dextrans [8], while those with molecular weight less than 40 kDa can be called oligodextrans [30]. However, some authors name high molecular weight dextran, low molecular weight dextran, and just dextran to generalize (as in this review) [31].

Some reports affirm the synthesis of dextran is affected by the amount of substrate—they already found the highest dextran production using sucrose between 10% and 20% [12,32], because sucrose causes an inhibitory effect that affects the production of the EPS [33]. However, the variations in the molecular weight and the types and proportions of branches in each dextran depend on the producing strain (or enzyme) and the fermentation (or synthesis) conditions, making each glucan complex and different [15,34]. Table 1 compiles studies that report the synthesis of dextrans by different bacteria, in which a variation in the molecular weight and the branches including dextrans produced by bacteria of the same genus is appreciated. For example, the genus *Leuconostoc mesen-*

teroides generally synthesizes dextrans with a main chain linked by α -(1 \rightarrow 6) bonds and branches with α -(1 \rightarrow 3) bonds [12]; however, the study by Sawale and Lele [16] reported that the UICT/L18 strain *Leuconostoc mesenteroides* synthesized a branched dextran with α -(1 \rightarrow 4) bonds. Siddiqui et al. [35] stated that the *Leuconostoc mesenteroides* KIBGE-IB22 strain produced a branched dextran with α -(1 \rightarrow 3) and β -(2 \rightarrow 6) bonds. However, most of the dextrans synthesized by LAB (i.e., *Leuconostoc*, *Lactobacillus*, and *Weissella*) have only α -(1 \rightarrow 6) and α -(1 \rightarrow 3) bonds with percentages between 52% and 97% and 3% and 48%, respectively.

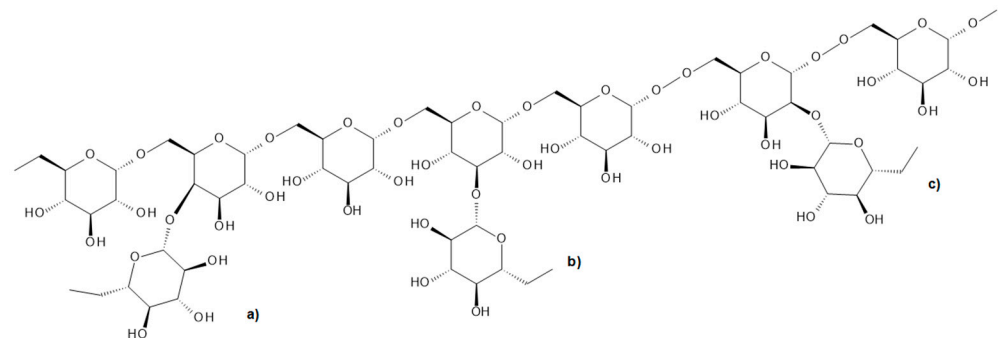


Figure 3. Structural model of dextran. Backbone formed by D-glucose units with α -(1 \rightarrow 6) bonds and different branching bonds: (a) α -(1 \rightarrow 4), (b) α -(1 \rightarrow 3), and (c) α -(1 \rightarrow 2).

There are other factors that affect both the molecular weight and the branching of dextran; for example, if fermentations with more than 25 °C are used, dextrans with greater branching are produced [36,37], while at temperatures lower than 25 °C, they are obtained with higher molecular weight [23,38]. In addition, with the increase in the concentration of sucrose, the yield of dextran decreases, but so does its degree of branching [37,39]. The commercial dextran synthesized by *Leuconostoc mesenteroides* NRRL B512 became the most important glucan due to its stability caused by composition of 95% α -(1 \rightarrow 6) bonds and 5% branches with α -(1 \rightarrow 3) bonds [21].

Table 1. Dextrans synthesized by lactic acid bacteria (LAB) isolated from different sources.

LAB			Substrates	Dextran		Reference
Genus	Subspecies	Source		Molecular Weight	Linkages	
<i>Leuconostoc mesenteroides</i>	SD1	<i>Agave salmiana</i>	Sucrose 10%		α -(1 \rightarrow 6) 93% α -(1 \rightarrow 3) 7%	[12]
	SD23	<i>Agave salmiana</i>	Sucrose 10%		α -(1 \rightarrow 6) 95% α -(1 \rightarrow 3) 5%	
	SF2	<i>Agave salmiana</i>	Sucrose 10%		α -(1 \rightarrow 6) 94% α -(1 \rightarrow 3) 6%	
	SF3	<i>Agave salmiana</i>	Sucrose 10%		α -(1 \rightarrow 6) 74% α -(1 \rightarrow 3) 26%	
	NRRL B512		Milk permeate 5%	<10 kDa		[31]
	NRRL B512		Sucrose 3%	<40 kDa		
	NRRL B512		Molasses			[40]
	NRRL B512		Cheese whey 6%			
	NRRL B512		Molasses + Cheese whey 2–10%			
	CM9	Camel milk	Sucrose 2%	230 MDa		[29]
	CM30	Camel milk	Sucrose 2%	390 MDa		
	SM34	Sheep milk	Sucrose 2%	210 MDa		
	RTF10	Meat products	Sucrose 2%	440 MDa		

Table 1. Cont.

LAB			Substrates	Dextran		Reference
Genus	Subspecies	Source		Molecular Weight	Linkages	
	BA08	Fermented rice batter	Whey + Sucrose 5%		α -(1→6) 93% α -(1→3) 7%	[14]
	KIBGE-IB22	Indigenous source	Sucrose 10%	15–20 MDa	α -(1→6) α -(1→3) β -(2→6)	[35]
	KIBGE-IB22M20	Mutant	Sucrose 10%	25–40 MDa	α -(1→6) α -(1→3)	
	BD1710		Tomato juice + Sucrose 15%	635 kDa	α -(1→6) 94% α -(1→3) 6%	[41]
	ATCC 10830		Residual pineapple juice + Sucrose 15%	960 kDa		[42]
	AA1	Fermented cabbage	Sucrose 10%	10–40 MDa		[15]
	NRRL B-1149		Sucrose 10% + Maltose 5%		α -(1→6) 52% α -(1→3) 48%	[43]
	UICT/L18	Fermented idli batter	Sucrose 22%	970 kDa	α -(1→6) α -(1→4)	[16]
<i>Leuconostoc carnosum</i>	CUPV411	Apple must	Sucrose 2%	358 MDa	α -(1→6) α -(1→3)	[44]
<i>Leuconostoc citreum</i>	SK24.002	Fermented pickles	Sucrose 10%	46 MDa	α -(1→6) 56% α -(1→3) 44%	[17]
<i>Leuconostoc</i> sp.	LS1	Sauerkraut	Sucrose 15%			[45]
	LI1	Idli batter	Sucrose 15%			
<i>Lactobacillus mali</i>	CUPV271	Ropy slime of cooked ham	Sucrose 2%	123 MDa	α -(1→6) α -(1→3)	[44]
<i>Lactobacillus sakei</i>	MN1	Meat products	Sucrose 2%	170 MDa		[29]
<i>Lactobacillus plantarum</i>	DM5	Ethnic fermented beverage	Sucrose 5%		α -(1→6) 87% α -(1→3) 13%	[46]
	LS3	Stool samples	Sucrose 15%			[47]
<i>Lactobacillus gasseri</i>	LV1	Vaginal swabs	Sucrose 15%			
	LV2	Vaginal swabs	Sucrose 15%			
	LS1	Stool samples	Sucrose 15%			
<i>Lactobacillus acidophilus</i>	LV3	Vaginal swabs	Sucrose 15%			
	LV4	Vaginal swabs	Sucrose 15%			
	LV5	Vaginal swabs	Sucrose 15%			
<i>Lactobacillus fermentum</i>	LS2	Stool samples	Sucrose 15%			
<i>Lactobacillus satsumensis</i>	NRRL B-59839	Water kefir grains	Sucrose 20%		α -(1→6) 55% α -(1→3) 45%	[48]
<i>Weissella cibaria</i>	27	Kimchi	Sucrose 20%	12 MDa	α -(1→6)	[49]
	10M		Sucrose 0.5 M	5–40 MDa		[50]
	YB-1	Pickle cabbage	Sucrose 5%	390 kDa	α -(1→6) 96% α -(1→3) 4%	[51]
	RBA12	Pummelo	Sucrose 2%		α -(1→6) 97% α -(1→3) 3%	[13]
	11GM-2	Sour milk	Sucrose 20%	>20 MDa	α -(1→6) 95% α -(1→3) 5%	[52]
	JAG8	Apple peel	Sucrose 10%	800 kDa		[53]

Table 1. Cont.

LAB			Substrates	Dextran		Reference
Genus	Subspecies	Source		Molecular Weight	Linkages	
	JAG8	Apple peel	Sucrose 2%	177 kDa	α -(1→6) 93% α -(1→3) 7%	[54]
	MG1		Sucrose 10%		α -(1→6)	[55]
	CMGDEX3	Cabbage	Sucrose 15%	>2 MDa	α -(1→6) 97% α -(1→3) 3%	[56]
<i>Weissella confusa</i>	PP29	Romanian yoghurt	Sucrose 8%	120–870 kDa	α -(1→6) 96% α -(1→3) 4%	[57]
	PP29	Romanian yoghurt	Milk + Sucrose 8%	120–250 kDa	α -(1→6) 96% α -(1→3) 4%	
	R003	Sugar cane juice	Sucrose 10%	10 MDa	α -(1→6) 97% α -(1→3) 3%	[58]
	QS813	Sourdough starters	Sucrose 5%	160 MDa	α -(1→6) 97% α -(1→3) 3%	[59]
	A3/2-1	Fermented cassava	Sucrose 10%	>20 MDa	α -(1→6) 97% α -(1→3) 3%	[52]
	A4/2-1	Fermented cassava	Sucrose 10%	>20 MDa	α -(1→6) 97% α -(1→3) 3%	
	F3/2-2	Fermented cassava	Sucrose 10%	>20 MDa	α -(1→6) 97% α -(1→3) 3%	
	E5/2-1	Fermented cassava	Sucrose 10%	>20 MDa	α -(1→6) 97% α -(1→3) 3%	
	G3/2-2	Fermented cassava	Sucrose 10%	>20 MDa	α -(1→6) 97% α -(1→3) 3%	
	8CS-2	Sour milk	Sucrose 10%	>20 MDa	α -(1→6) 97% α -(1→3) 3%	
	11GU-1	Sour milk	Sucrose 10%	>20 MDa	α -(1→6) 97% α -(1→3) 3%	
	11GT-2	Sour milk	Sucrose 10%	>20 MDa	α -(1→6) 97% α -(1→3) 3%	
	K1-Lb5	Kimchi	Sucrose 20%	1158 kDa	α -(1→6) α -(1→3)	[60]
	Cab3	Fermented cabbage	Sucrose 5%			[61]
<i>Weissella</i> sp.	TN610	Pear	Sucrose 4%	180 kDa	α -(1→6) 96% α -(1→3) 4%	[62]

Some researchers prefer the enzymatic use to produce dextran due to the advantages it presents over fermentation; for example, microbial enzymes can be easily modified by molecular engineering, they do not need growth factors such as yeast and meat extracts, and they produce specific and pure metabolites, which translates into a reduction in processing costs [63,64]. Table 2 shows high and low molecular weight dextrans produced via enzymatic. In these studies, most of the enzymes have been modified to synthesize high molecular weight dextrans (up to 23 MDa) [65]; however, enzymes have also been designed to directly produce low molecular weight dextrans or even to achieve the synergic interaction between enzymes to obtain low molecular weight dextrans with varied molecular weights [66]. Most of the characteristics of dextrans produced via enzymatic depend on the type of enzyme (source or method of obtaining it); however, the molecular weights are also directly related to the concentration of the substrate [67]. On the other hand, the dextrans obtained by this via report a variation between α -(1→6) and α -(1→3) bonds; specifically, they show a decrease in the percentage of α -(1→6) bonds compared to the dextrans obtained by fermentation. It even allowed obtaining totally linear dextrans [65] and with α -(1→6) and α -(1→2) bonds [68]. In general, the modification or transformation of enzymes by engineering makes it possible to obtain dextrans with desired characteristics.

Table 2. Dextrans synthesized by enzymes isolated from different sources.

Enzyme		Microorganisms		Substrates	Dextran		Reference
Type	Obtaining	Genus	Subspecies		Molecular Weight	Linkages	
Glucansucrase GTF180	Isolated	<i>Leuconostoc reuteri</i>	180	Maltose 100 mM + Sucrose 100 mM	~23 MDa	α -(1→6) 78% α -(1→3) 22%	[65]
Glucansucrase L940G	Mutated		180	Maltose 100 mM + Sucrose 100 mM	~17 MDa	α -(1→6) 85% α -(1→3) 15%	[65]
Glucansucrase L940C	Mutated		180	Maltose 100 mM + Sucrose 100 mM	~17 MDa	α -(1→6) 74% α -(1→3) 26%	[65]
Glucansucrase L940A	Mutated		180	Maltose 100 mM + Sucrose 100 mM	~19 MDa	α -(1→6) 84% α -(1→3) 16%	[65]
Glucansucrase L940S	Mutated		180	Maltose 100 mM + Sucrose 100 mM	~20 MDa	α -(1→6) 84% α -(1→3) 16%	[65]
Glucansucrase L940M	Mutated		180	Maltose 100 mM + Sucrose 100 mM	~19 MDa	α -(1→6) 72% α -(1→3) 28%	[65]
Glucansucrase L940E	Mutated		180	Maltose 100 mM + Sucrose 100 mM	~19 MDa	α -(1→6) 73% α -(1→3) 27%	[65]
Glucansucrase L940F	Mutated		180	Maltose 100 mM + Sucrose 100 mM	~20 MDa	α -(1→6) 93% α -(1→3) 7%	[65]
Glucansucrase L940W	Mutated		180	Maltose 100 mM + Sucrose 100 mM	~6 MDa	α -(1→6) 100%	[65]
Dextransucrase B-512FMC	Mutated	<i>Leuconostoc mesenteroides</i>	B-512FMC	Sucrose 20 mM	20–341 kDa	-	[67]
Dextransucrase B-512FMC	Mutated		B-512FMC	Sucrose 50 mM	49–431 kDa	-	[67]
Dextransucrase B-512FMC	Mutated		B-512FMC	Sucrose 100 mM	63–514 kDa	-	[67]
Dextransucrase B-512FMC	Mutated		B-512FMC	Sucrose 200 mM	126–787 kDa	-	[67]
Dextransucrase B-512FMC	Mutated		B-512FMC	Sucrose 1000 mM	1645 kDa	-	[67]
Dextransucrase FT045B- Dextranase	Isolated	<i>Leuconostoc mesen- teroides</i> <i>Penicillium</i>	FT045Bsp.	Sucrose 400 mM	~92 kDa	α -(1→6) 98% α -(1→2) 2%	[68]
Dextransucrase (DE3)/pET28- dexYG	Engineered	<i>Escherichia coli</i>	BL21	Sucrose 10%	5 kDa	-	[66]
Dextransucrase (DE3)/pET28- dexYG-Dextranase	Engineered	<i>Escherichia coli</i> <i>Penicillium aculeatum</i>	BL21-	Sucrose 10%	10–20 kDa	-	[66]
Dextransucrase WcCab3	Isolated	<i>Weissella confusa</i>	Cab3	Sucrose 5%	178 kDa	α -(1→6) 97% α -(1→3) 3%	[69]

On the other hand, low molecular weight dextrans are obtained mainly through acid hydrolysis of a high molecular weight dextran; however, there are studies that use enzymatic hydrolysis to produce them [66,70], as shown in the Table 3. In these studies, enzymes derived from LAB were modified or cloned to hydrolyze high molecular weight dextrans to shorter chain dextrans (up to 500 Da) [71]. The dextrans obtained specifically presented α -(1→6) and α -(1→2) bonds in different proportions depending on the enzyme and the substrate (dextran). Furthermore, the cloning of enzymes allowed them to be used not only for dextran hydrolysis, but also to polymerize high molecular weight dextrans from short chain dextrans [72].

Table 3. Dextrans synthesized by hydrolysis enzymatic.

Enzyme		Microorganisms		Substrates	Dextran		Reference
Type	Obtaining	Genus	Subspecies		Molecular Weight	Linkages	
Dextranase	Isolated	<i>Penicillium</i>	Sp.	Dextran 40 kDa	5–8 kDa	-	[70]
α -1,2 transglucosidase	Engineered	<i>Leuconostoc mesenteroides</i>	NRRL B-1299	Dextran 70 kDa	0.5 kDa	α -(1→6) 75% α -(1→2) 25%	[71]
α -1,2 transglucosidase	Engineered	<i>Leuconostoc mesenteroides</i>	NRRL B-1299	Dextran 70 kDa	1 kDa	α -(1→6) 68% α -(1→2) 32%	[71]
Transglucosidase GBD-CD2	Cloned	<i>Leuconostoc mesenteroides</i>	NRRL B-1299	Dextran 70 kDa + Sucrose 292 mM	10 kDa	α -(1→6) 62% α -(1→2) 38%	[72]
Transglucosidase GBD-CD2	Cloned	<i>Leuconostoc mesenteroides</i>	NRRL B-1299	Dextran 70 kDa + Sucrose 292 mM	40 kDa	α -(1→6) 63% α -(1→2) 37%	[72]
Transglucosidase GBD-CD2	Cloned	<i>Leuconostoc mesenteroides</i>	NRRL B-1299	Dextran 70 kDa + Sucrose 292 mM	70 kDa	α -(1→6) 62–67% α -(1→2) 33–38%	[72]
Transglucosidase GBD-CD2	Cloned	<i>Leuconostoc mesenteroides</i>	NRRL B-1299	Dextran 70 kDa + Sucrose 292 mM	70 kDa	α -(1→6) 81–88% α -(1→2) 12–19%	[72]
Transglucosidase GBD-CD2	Cloned	<i>Leuconostoc mesenteroides</i>	NRRL B-1299	Dextran 70 kDa + Sucrose 292 mM	2000 kDa	α -(1→6) 64% α -(1→2) 36%	[72]

4. Properties of Dextran

Variations in dextran characteristics (e.g., molecular weight and branching) cause its properties to be different [15,34]. The main chain of dextran with α -(1→6) bonds adopts a helical shape, which is modified by the presence of branches (α -(1→2), α -(1→3) or α -(1→4)), such that the linear structure of glucan is repeatedly folded [73–75].

The solubility and rheological properties of dextran are affected by its molecular weight and branching [76]. The solubility of polymers refers to the interaction of the molecule with water through interactions by hydrogen bridges [77]. Some research asserts that if the dextran molecule were totally linear (without branches), it would be totally soluble, because its hydroxy groups (–OH) would be exposed to interact with water molecules [78]. Other investigations affirm that the greater the number of branches, the greater the solubility of the dextran due to the increase in amorphous areas in the molecule that favor water adsorption and retention [73–75]. There are even reports that, in general, all low molecular weight polysaccharides have a higher solubility compared to long chain polysaccharides [43]. There is no direct relationship between the characteristics of the molecule and the variation of the properties [14,35,41,68,79]. However, regardless of the degree of solubility, dextrans are considered soluble EPS due to their ability to incorporate large amounts of water and form hydrogels [80].

The rheology and viscosity of polymers show their behavior as flow or deformation under an applied force, respectively [81], which is associated with –OH groups that easily interact with other molecules through hydrogen bonds, which are they break during shear [80]. Generally, the viscosity of dextran is directly related to the concentration and the shear rate, which means that at low concentrations they have a Newtonian behavior (independent of the shear rate) and at high concentrations their behavior is non-Newtonian (or pseudoplastic) [29]. Other studies show that the viscosity is also in direct relation to the molecular weight of the dextran, since as one increases, the other increases [82].

On the other hand, the flexibility of the polymers is determined as a function of the temperature; however, the temperatures vary depending on the intermolecular forces, crystallinity, and the size of the polymer [83]. Linear amorphous polymers have characteristics like glass at low temperatures—that is, little flexibility due to the zero mobility of the polymer chains [84]. With increasing temperature, they tend to become leathery (at the glass transition temperature, T_g), then rubbery and finally melt (at the melting temperature, T_m) [83]. During this transformation process, polymers show their most flexible point [84]. In crystalline polymers, the T_g is high due to intermolecular forces between the polymer

chains. In short chain polymers, the T_m is low because the entropy is low, whereas long chains tend to be less mobile with high entropies, so the T_m is high [83].

5. Concluding Remarks and Future Perspectives

The production of dextran occurs mainly by a fermentation with LAB in a medium with sucrose; however, the enzymatic route has been used because it is a direct method in which other products or metabolites are not produced. The enzymatic pathway has also allowed the modification of enzymes to produce dextrans with specific desired characteristics. The characteristics of dextran depend on the LAB or enzyme of origin, which makes each dextran unique in terms of molecular structure, molecular weight, and branching, which cause variations in the viscosity and flexibility, and thermal and rheological properties. In addition, these properties vary depending on the temperature, concentration, and force applied to each dextran, which allows its application in different areas such as food, pharmaceuticals, cosmetics, and research.

In medicine, high molecular weight dextran (between 40 and 70 kDa) has been used as an extender, anticoagulant, antithrombotic, osmotic agent, and intravenous plasma lubricant; in addition, it is used as a cryopreservative for vaccines and organs [8,28]. In the cosmetic industry, dextran has been used as a thickening and moisturizing agent, and its reducing property allows it to be used as an anti-aging agent. In the research area, dextran is useful to generate chromatography matrices, immobilize biosensors, generate nanoparticles, and form emulsions [28].

However, the most explored application of dextran is in the food industry, as it is used in baking and confectionery due to its moisturizing, stabilizing, and preserving effects, improving the flavor, texture, and consistency of ice creams, sweets, breads, flours, and jellies. In meat, vegetable, and cheese products, it has been added to retard oxidation; therefore, they are preservatives of texture, aroma, and flavor [8,15,28,85]. In addition, dextran has been proposed to be used as coatings or biodegradable film-forming agents [86,87], and as potential prebiotics (low molecular weight dextrans) [71,88].

The versatility of dextran has attracted attention in the past decade, and for this reason, the sources of obtaining LAB and the manipulation of enzymes that produce it have increased in such a way that the variety of dextrans has also increased its applications. However, the full characterization of each dextran produced is still incomplete and it would be worth studying so that they could compete with commercial dextran from *Leuconostoc mesenteroides* NRRL B512.

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