Xylitol: metabolism, microbial production and perspective in polymer substrates utilization

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1. Introduction

Xylitol, a naturally occuring five carbon sugar polyalcohol, is a constituent of biomass of both plant and vegetable origins and has been obtained commercially by chemical method since 1970 (1). This polyol (Fig. 1) is presently an interesting product for the food and pharmaceutical industries owing to its high sweetening power and anticariogenicity. It is used as sugar substitute and coating agent in the production of food products (jams, chocolate, jellies, gelatin desserts) for diabetic patients and formulation of pharmaceutical products (toothpastes and drugs) (1,2). On the other hand, xylitol has its disadvantages due to slow absorption in the intestine and slight laxative effect and these reasons restrict its daily intake up to 50g. Besides its sweetening power, xylitol possesses many other advantageous physico-chemical properties such as high solubility (680 g/kg solution), low melting point 93-94.5°C and it does not easily crystallize (1-3). Furthermore, it does not undergo Milliard type reaction with amino acids and it is microbiologically stable (1,3,4).

The worldwide production of xylitol is only about 5000 tons/year and the price is about ten-fold that of sucrose or sorbitol. The raw-materials from which xylitol is obtained industrially are wood pulp from paper processing industry, lignocellulosic materials (beech and other hardwood chips), plant biomass and other agricultural by-products. These raw-materials generally contain about 20-35% of xylan, a xylose polymer made up of D-xylose units (1,3,4). The existing chemical method of xylitol production involves the hydrolysis of xylan-hemicellulose portion of the plant biomass to obtain D-xylose for catalytic hydrogenation to xylitol and subsequently purifying by crystalization to purity of more than 98.5% (4). This conventional

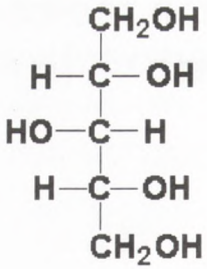

Fig. 1. Chemical structure of xylitol.

method of xylitol production poses a significant technical problem generated by poor selectivity, leading to a complex mixture of polyols and sugars that are subjected to expensive refining treatments. Besides, the chemical process is performed at high temperature and high pressure, which increases the cost of production.

In this regard, the discovery of the xylose-xylitol conversion by microorganisms that belong to the yeast-family (5) and the applicability of these strains have opened new perspectives for the fermentative replacement of the chemical method. The microbial synthesis of xylitol is becoming more attractive due to its cheapness compared to the chemical method. Furthermore, it does not necessary require a pure D-xylose solution and does not leave behind toxic residues of catalysis when compared to the chemical method. The ability of xylose-fermenting yeast to ferment complex sugar polymer substrates commonly found in lignocellulosic materials after pretreatment is important for their potential use in the fuel industry and also in the production of xylitol. It is the purpose of this review to discuss the recent findings concerning microbial production of xylitol by D-xylose fermenting yeasts, xylitol metabolism and genetic engineering techniques so far applied in improving the strains, as well as the prospects of utilizing processed lignocellulosic materials for xylitol production.

2. Xylitol metabolism and its microbial production

2.1. Xylitol metabolism

Xylitol, which is a normal intermediate product of human and animal metabolism, was first discovered in 1956 by Hollman and Touster in the mammalian liver. These authors showed that the reduction of xylose to xylitol is an NADP -dependent system (1). In the same fashion, the formation of keto-pentoses in *Candida utilis*, an aerobic yeast, was also demonstrated in 1969 by Horecker as a general way of how polyols are formed in microorganisms. Recently, several natural yeasts have been reported to produce xylitol from D-xylose with different capabilities. The yeasts include: *Candida*

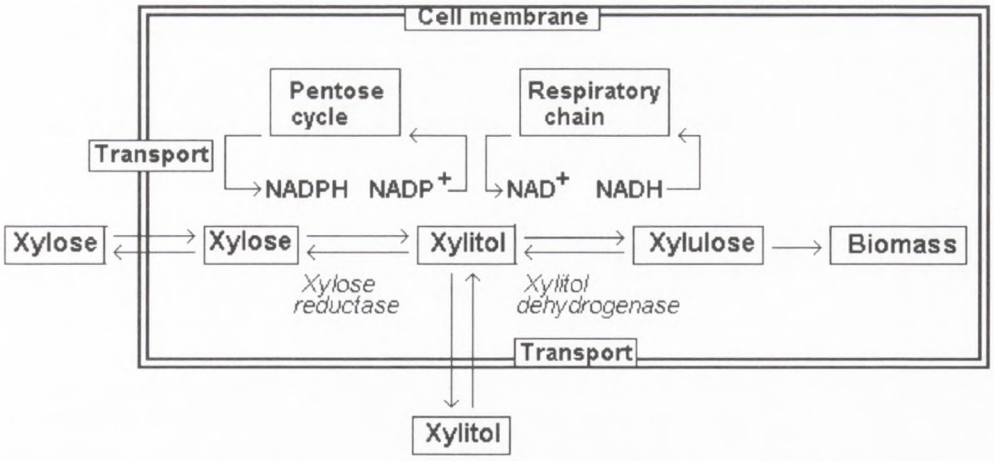

Fig. 2. Scheme of initial step in the D-xylose metabolism by xylitol producing yeasts.

shehatae, *Candida tropicalis*, *Candida guilliermondii*, *Candida boidinii*, *Candida parapsilosis*, *Candida mogii* and *Debaromyces hansenii* Y-7426 (2,3,6-9). Other yeasts that belong to the xylose-fermenting yeast like *Pichia stipitis* and *Pachysolen tannophillus* are capable of utilizing D-xylose solely for their growth and production of ethanol with negligible amounts of by-products e.g. xylitol (15).

The metabolic mechanism of D-xylose reduction to xylitol and its accumulation by D-xylose -fermenting yeasts have been explained by the differences in the nature of the initial steps of xylose metabolism that exist in these organisms and termed a simple enzymatic process. In Figure 2 (8), the scheme of D - xylose metabolism during xylitol production by yeasts is shown. According to this scheme, the oxidoreductive conversion of D-xylose to D-xylulose is catalyzed by the sequential action of two enzymes — xylose reductase (XR) [EC. 1.1.2.1] and xylitol dehydrogenase (XDH) [EC.1.1.1.9.]. In the first step, xylose reductase (XR) converts xylose to xylitol. The formed xylitol is either excreted from the cell into the culture medium or oxidized in the cell to D-xylulose by another NAD-dependent enzyme — xylitol dehydrogenase (XDH) [EC. 1.1.1.9.]. D-xylulose is subsequently phosphorylated to fructose-6-P by the action of the enzyme xylulokinase and degraded through the pentose phosphate pathway and the Embden-Meyerhof-Parnas pathway (6,10,15). Although xylose metabolism of these xylose — fermenting yeasts is still not fully understood, it has been claimed that the existence of NADH-linked xylose reductase is a prerequiste for the anaerobic alcoholic fermentation of the hemicellulosic hydrolysate by these yeasts. Semi-aerobic metabolism of xylose *via* NADPH-linked xylose reductase leads to an imbalance in the rate of NAD/NADH (6,10). Under this condition, the rate of the oxidative pathway is restrained and this leads to accumulation of NADH in

the second step of the xylose metabolism because the reducing equivalents cannot be reoxidized by the xylose reductase-catalyzed reaction. This fact leads to an increase of the metabolic reduction charge which, in turn, blocks the activity of xylitol dehydrogenase and thus results in xylitol accumulation in the medium (4). Xylitol accumulation drops with the increase in oxygen uptake (11).

2.2. Physiology of xylose-xylitol producing yeast strains

Xylose-xylitol producing yeast strains exhibit various closely related physiological behaviour during cultivation. An example is the characteristic behaviour of *C. shehatae* grown initially under strict aerobic conditions and then shifted to anaerobic conditions. Under these conditions, neither ethanol nor xylitol was produced under fully aerobic conditions. This indicated that *C. shehatae* was a Crab-tree negative yeast, which seemed to be applicable to other xylose-xylitol producing yeasts; all the carbon sources were respired. On the other hand, upon changing the growth conditions to anaerobic, the yeast almost ceased to grow but it still continued to assimilate xylose and produce fermentative metabolites (ethanol) and other secondary metabolites (xylitol) as by-products (6).

Recently, a xylose-xylitol conversion recombinant strain *S. cerevisiae* carrying a gene encoding xylose reductase (XR) of *Pichia stipitis* CB 6054 has been cloned (12). This strain efficiently converted xylose to xylitol with a conversion efficiency of over 90%. The comparison of the cDNA copies of XYL1 gene showed that the genomic XYL1 contained no introns and an XR monomer of 318 amino acids (35.985) was encoded by an open reading frame of 954bp. The amino acid sequence of the *P. stipitis* XR is similar to several aldose reductases, suggesting that *P. stipitis* XR is a part of the aldoketose reductase superfamily found in *S. cerevisiae* transformed with the XYL1 gene. Generally, it has been claimed that the yeast *S. cerevisiae* is unable to assimilate D-xylose, therefore it cannot produce xylitol. However, studies carried out with the yeast *S. cerevisiae* have demonstrated that some of these strains utilize xylose with different efficiencies in the presence of other sugar substrates and convert xylose into xylitol (13,14). The greatest amount of consumed xylose (69% over 7 days) was attained when sugar substrates such as D-rybose were co-metabolized. This fact indicates a need to search for a natural strain of *S. cerevisiae*, which is capable of producing xylitol in large amounts because *S. cerevisiae* does not seem to possess xylose dehydrogenase activity (14). When [^{14}C] xylose was utilized in the presence of D-xylose under anaerobic conditions, the radioactive label was detected mainly in xylitol and not in the small amount of ethanol produced. Under aerobic conditions, the radioactive label was distributed between xylitol ($61.3 \pm 0.8\%$), CO_2 ($2.6\% \pm 2.3\%$) and biomass ($1.7 \pm 0.6\%$). Again, this demonstrates a physiological or biochemical difference between *S. cerevisiae* and other xylose-xylitol fermenting yeasts and apparently shows that *S. cerevisiae* possesses a pathway which completely oxidizes xylose to xylitol

in the presence of other sugar substrates. As demonstrated, xylose was assimilated by means of low and high affinity glucose transport system. Cells exposed to a mixture of xylose and ribose for 2 days showed a high-affinity transport system. On the other hand, *P. stipitis* NRRL Y-7124 and CBS 7126 have been shown to assimilate xylose and glucose with a high and low-affinity system, while glucose is taken up with one up-take system (15). The low- affinity system is shared by xylose and glucose, whereas the high-affinity system for xylose is non-competitively inhibited by glucose. In contrast, *P. stipitis* and *C. shehatae* CBS 2779 use a facilitated diffussion system in addition to the proton symport mechanism (15).

3. Biotechnological production of xylitol

3.1. Factors affecting xylitol production

3.1.1 Effect of oxygen-transfer rate

The main technological parameters influencing the bioconversion of xylose to xylitol have been associated with the concentration of dissolved oxygen in the medium, which plays a significant role. Under anaerobic conditions, xylose cannot be assimilated by yeast without NADH-linked xylose reductase. Due to this fact, the cell growth is hindered and no accumulation of xylitol but and under strict aerobic conditions, the fermentation is directed towards biomass production. Therefore, accumulation of xylitol is enhanced by either anoxic condition or limited aeration rate (3). The effect of an oxygen transfer rate (OTR) decrease on a *C. shehatae* culture has been evaluated. Under oxygen limitation the xylose metabolism is intrisically respiro-fermentative and this type of metabolism is characterized by simultaneous oxygen uptake rate, ethanol production and low biomass formation (6). Another factor limiting xylitol production is the complicated physiological behaviour of xylose-xylitol fermenting yeasts, especially the assembling of the enzymes responsible for its conversion. *Candida tropicalis* IFO 0618 has been shown to possess three D-xylose reductase (XR) isomers and xylitol dehydrogenase (XDH) and it does not have xylose isomerase (7,28). This strain showed higher activity of NAD^+-linked XDH and lower actvity of $NADP^+$-linked XDH. On the other hand, it had higher activity of NADPH-linked XR and lower activity of NADH-linked XR. Examination of the activities of NAD^+-linked XDH to that of NADPH-linked XR showed that the former was about two-fold that of the latter (7). This type of complicated enzyme assembling does probably exist in other xylitol producing yeasts. This fact led to the suggestion that in the presence of sufficient NADPH and NADH, xylitol is produced from D-xylose and the formed xylitol could be easily dehydrogenated to D-xylulose and utilized preferentially for ethanol production. This is one of the mechanisms limiting xylitol production.

3.1.2. The effect of initial D-xylose concentration

The initial D-xylose concentration, which is the basic carbon source in this process, as well as initial microbial cell density loading during cultivation have been shown to play a crucial role for the specific production rate of xylitol (7,16). Concentrations from 20-300g/dm^3 D-xylose in the medium have been investigated (7,16,17) and it was found that the maximum productivity of xylitol could be attained at 50g/dm^3 D-xylose. On the other hand, Cao et al. (16) studied the effect of high cell density loading in association with high D-xylose concentration on the formation of xylitol by *Candida* sp. They found that the rate of xylitol production increased with increasing yeast cell density. At the optimal temperature and pH levels, a high cell density loading of 26mg/cm^3 produced about 210g/dm^3 xylitol from 260 g/dm^3 D-xylose, which gave a yield of 81% of the theoretical value. Studies with *C. tropicalis* (4) showed that at higher D-xylose concentrations above 200g/dm^3, the growth of the yeast was inhibited. On the other hand, Horitsu et al. (7) studied the influence of culture medium conditions on xylitol formation by *Candida tropicalis* and optimized the volumetric production rate by the Box-Wilson method. In this regard, D-xylose concentration, yeast extract and k_La were chosen as independent factors and the maximum xylitol production rate of 2.67 g/dm^{-1} · h was obtained. Optimal levels of these parameters were found to be in the range of 172.0g/dm^3 D-xylose, 21 g/dm^3 yeast extract and a k_La of 451.5 l/h with xylitol yield of 110 g/dm^3. The highest xylitol yield so far obtained on pure xylose medium with natural strains such as *C. guilliermondii* and *Candida* sp. *B 22* were 0.826 and 0.845g/g, respectively, while the theoretical yield was calculated to be 0.917 g/g D-xylose. In both experiments, cultivations were carried out with the initial xylose concentration of 249-300 g/dm^3 and xylitol concentrations of 221-249 g/dm^3 were obtained (2,18).

3.1.3. The effect of nitrogen sources

The nature of nitrogen sources of both organic and inorganic origin (urea, ammonium salts, yeast extracts, casamino acids in different combinations) and cultivation temperatures apart from agitation and aeration rate also play an important role in xylitol production (9,19). Xylitol production rate, average specific productivity and yield vary according to the kind of N source, obeying the following sequences: $NH_4CL > (NH_4)SO_4 >$ urea (19). Generally, inorganic N sources are preferred to the nitrogen of organic origin. Lu et al. (20), also examined the effect of different nitrogen sources on the production of xylitol by *Candida* sp. *L102*. They showed that during the cultivation of *Candida* sp. *L102* urea or glycine gave the highest specific productivity of xylitol of 0.46 g/g·h, while the highest yield (87.7%) was attained with ammonium phosphate. On the other hand, the lowest xylitol yield was obtained with the use of asparagine as an organic nitrogen source. According to Barbosa et al. (21), when urea and yeast extract were used under oxygen

— limited conditions, about 77.2 g/dm^3 xylitol was produced from 104 g/dm^3 xylose in 75 h. This gave a xylitol yield of 0.74 g g^{-1} and an average specific rate of xylitol production of 0.22 $g \cdot g^{-1} \cdot h^{-1}$.

3.1.4. The importance of physico-chemical conditions

The importance of the physico-chemical conditions (temperature and pH value) and the concentration of certain chemical cofactors (Mg^+) in the culture medium cannot be neglected and it has been investigated. These parameters have been shown to affect xylitol production, although various xylitol producing yeast strains have their specific condition. Generally, cultivation temperature and pH profiles for the production of xylitol vary from 30-37°C and 4.5-6, respectively (2,3,9). An exception is a specific yeast strain *C. tropicalis* investigated by Silva et al. (4), which showed maximum productivity of xylitol at a low pH value of 2.5. This yeast strain behaviour differs from other xylitol producing yeast strains so far investigated and can be economically useful due to non-sterile cultivation. On the other hand, the concentration of magnesium ions has been shown to influence the direction of the metabolic flow and thereby, alters carbon flux and product formations (xylitol or ethanol) by *Pichia stipitis*, which naturally produces only ethanol as the final product (22). Mahler and Guebel (22) studied the influence of Mg^{2+} concentrations in the medium, and found that at low concentrations of Mg^{2+} (1mM), about 49% of the carbon flux to ethanol was re-channelled to xylitol production and this was accomplished through NADH intracellular accumulation or regeneration.

3.1.5. Strain manipulation (modification) and immobilization

In the production of xylitol, both conventional mutagenesis and recombinant DNA techniques have been used to improve the yield of xylitol either by obtaining a yeast strain deficient in one or more enzymes of xylitol metabolism or cloning and expression of xylose reductase (XR) gene of *Pichia stipitis* CB 6054 into the host strain *S. cerevisiae* (2,15). A modified *Kluyveromyces marxianus* strain by mutagenesis accumulated xylitol with the yield of 0.68 $g \cdot g^{-1}$ from 120g/dm^3 xylose and the specific xylitol production rate attained was 0.13 $g \cdot g^{-1} \cdot h^{-1}$. Yeast cells immobilized in calcium alginate beads have been studied for continuous xylitol production. In this regard, Thonart et al. (23), used *Pachysolen tannophillus* and attained a yield of 0.6 $g \cdot g^{-1}$ xylose, but the volumetric productivity was low and amounted to 0.05 $g \cdot dm^{-1} \cdot h^{-1}$. There are several Japanese patents on the use of immobilized yeast for continuous production of xylitol. The highest volumetric productivity claimed in these patents was 7.5$g \cdot dm^{-1} \cdot h^{-1}$. Roca et al. (24) recently investigated production of xylitol in a packed-bed bioreactor with two Ca-alginate immobilized recombinant *S. cerevisiae* strains, harboring the XYL1 gene and exhibiting about 20-fold difference in xylose reductase activity. As reported, the volumetric productivity was in the range

of 3.4 and 5.8 g/l · h, respectively for low and high XR strains. These values are higher than the volumetric productivity (1g/dm^3) obtained with free recombinant strain.

Although the method of xylitol production has been termed a simple enzymatic process; there are seldom reports on this method of technological approach in the production of xylitol. Nevertheless, an ionized membrane reactor system constructed in a manner that it retains both the enzymes and cofactor in the bioreactor using an ultrafiltration membrane has been reported (25). A crude extract from *Candida pelliculosa* carrying xylose reductase and crude extract from *Methanobacteriun* sp. containing oxidoreductase were used for the oxidation and reduction of added NADPH. Hydrogen was used as a reducing agent. In this system, the activity of the cofactor was lost within few hours, but within the first four hours the xylitol yield amounted to 0.93 g/g · dm^3 D-xylose. Reports on this method of xylitol production should be interesting as not much has been done so far in this area of research.

3.2. Processed lignocellulosic material utilization

One of the objectives of this research is to utilize and develop a much cheaper method of xylitol production rather using forest and agricultural residues as substrates than pure D-xylose. Efforts to extend these studies have proved to be a success and recently a scale-up pilot plant has been developed for the production of xylitol from agricultural residues e.g. rice straw (Fig. 3) (26). The whole process involves pretreatment of the raw-material by hydrolysis followed by electrodialysis and reverse osmosis for the demineralization and concentration of the hydrolysates, respectively, prior to fermentation. Conventional yeast cells separations after fermentation are conducted either by centrifugation or filtration techniques. Cleaned broth is subsequently processed to recover purified xylitol by chromatographic techniques and crystalization (26).

In view of this fact, Roberto et al. (27) studied the formation of xylitol using agro-industrial residues such as sugarcane bagasse and rice straw-hemicellulosic hydrolysates containing an initial xylose concentration of 40g/dm^3. They obtained a yield of 0.70g/g, which was similar to that obtained with pure D-xylose as substrate by other authors (2,18). The problem encountered upon using of lignocellulosic hydrolysates in xylitol production is their complex nature and the ability of strains to grow in this medium due to the presence of other sugar substrates, which act as catabolite repressors, and other chemical agents (acetic acid, furfural and its derivatives) that might affect the viability of cells or invariably modify the general metabolism of yeast strains. Model experiments have been carried out with a mixture of pure D-xylose and other substrates found in lignocellulosic hydrolysates to alleviate the mechanism of xylitol formation by *C. guilliermondii* and *C. tropicalis* (10,28). In this regard, Felipe et al. (10), studied the effect of D-xylose mixture with glucose at a ratio of 4:1 (w/v) in the presence of

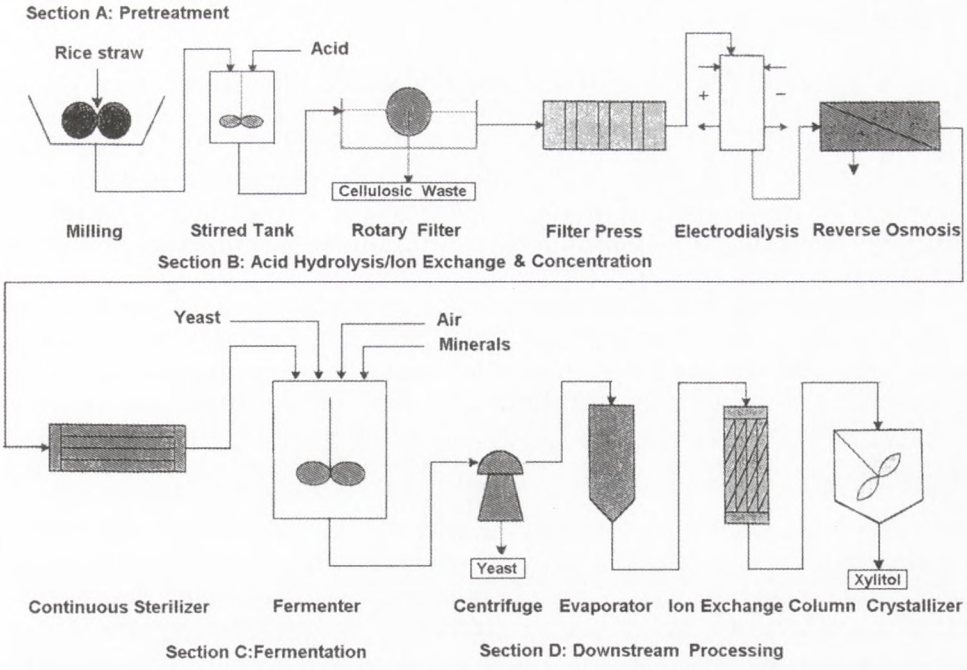

Fig. 3. Flow-sheet of xylitol production from processed lignocellulosic materials.

acetic acid at different concentrations on the formation of xylitol. They found that the concentration of acetic acid within the range of 1.5-12 g/dm^3 reduced the yield of xylitol to about 50% and inhibited the cell growth. However, at a lower concentration up to 1 g/dm^3, the presence of acetic acid stimulated the yield and productivity of xylitol with maximum values of 0.82 g/g and 0.57 g/dm^3 · h^{-1}, respectively. On the other hand, Yahashi et al. (28) examined the effect of glucose feed-rate on the production of xylitol in a batch-culture in the presence of D-xylose (35). It was found that feeding 10g/day/200cm^3 of D-glucose in a 2 dm^3 working bioreactor improved both the cell growth and xylitol production rate. After 42 h cultivation, xylitol concentration of 102.2g/dm^3, production rate of 2.43 g/dm^3 · h and yield of 0.68 were achieved. This method of cultivation shows the importance of cell mass and NADPH regeneration on xylitol production rate and yield. Different processes which involved simultaneous production of ethanol and xylitol directly from lignocellulosic hydrolysates by yeasts *C. tropicalis* and *Debaromyces hansenii* have also been described (3,4). Xylitol yields close to 0.9g/g xylose were achieved.

4. Conclusion

From the available data, it can be concluded that there is a growing interest in microbial production of xylitol due to its cheapness in comparison with the chemical method. The sweetening power and clinical importance of xylitol permit its use as sugar substitute and coating agent both in the production of food products (jams, jellies, gelatin desserts) for diabetic patients and formulation of pharmaceutical products (toothpastes and drugs), respectively.

It can be speculated that oxygen transfer-rate, xylose transport accross the cell membrane and oxidation of xylitol to D-xylulose are the rate-limiting factors in xylitol accumulation during fermentation. It seems that apart from the influence of xylose concentration, nitrogen concentration and its origin, pH value, inoculum cell density as well as aeration rate, other factors which might affect xylitol production rate are yet to be resolved. In this regard, efforts should be directed towards improving the characteristics of yeast strains by mutagenesis and recombinant technology and understanding the biochemical mechanism of the key enzymes responsible for xylitol formation. Furthermore, research should also be directed towards finding an enzymatic method of xylitol production as an alternative to microbial synthesis.

Due to the increasing cost of pure D-xylose acquisition from lignocellulosic materials (plant biomass) by the chemical method, it is worthy of note that microbial production of xylitol directly from processed polymer substrates of plant biomass creates a novel prospect for further reduction of the cost of production. To achieve this goal, adequate pretreatment of the plant biomass and adaptation of the yeast strains to grow in this medium are prerequisites for their universal and perspective utilization in microbial synthesis of xylitol.

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Summary

This article reviews the current concepts in microbial production of xylitol with pure D-xylose or processed lignocellulosic materials as substrates by yeast strains such as *Candida tropicals*, *C. guilliermondii* and *Debaromyces hansenii*. The importance of xylitol as sugar substitute and coating agent in the production and preparation of food and pharmaceutical products was presented. In addition, the metabolism of D-xylose to xylitol, physiology of the yeast strains and biotechnological parameters affecting the formation of xylitol were discussed.

Key words:
xylitol metabolism, xylitol production, xylitol, yeasts.

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