

Production of Pentoses by Micro-organisms

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Introduction

Pentoses are widely distributed in nature: they have important biological roles as components of biopolymers such as DNA, RNA, xylan and arabinan, as components of coenzymes (NAD, NADP, FAD, ADP, UDP, CDP, GDP), or as metabolic intermediates in, for instance, the pentose phosphate pathway, the uronic acid cycle, and in the assimilation of aldopentoses and pentitols in micro-organisms. Pentoses also exist as components of nucleoside antibiotics.

D-Ribose is used industrially for the chemical synthesis of riboflavin (Kuhn *et al.*, 1935) and has long been prepared from D-glucose by a chemical process involving several stages (Gehrke and Aichner, 1927). Recently developed methods of D-ribose production employ micro-organisms or microbial enzymes. Hydrolysis of RNA by microbial enzymes was first used. D-Ribose 5-phosphate is one of the major intermediates of the pentose phosphate pathway: thus micro-organisms were sought which would be able to produce and excrete D-ribose directly into the culture medium. Among those micro-organisms with this capability, transketolase (EC 2.2.1.1) mutants of *Bacillus* spp. have been used in particular for economic production of large amounts of D-ribose in the culture medium (Sasajima and Yoneda, 1971). The transketolase-deficient (*tkl*) mutant was improved by further mutation. The improved strains have been used widely during the past 10 years for the industrial production of D-ribose, replacing the chemical method used hitherto, and thereby avoiding the use of mercury which is essential for the electrolytic reduction required in the chemical process.

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Abbreviations: ADP, adenosine 5'-diphosphate; CDP, cytidine 5'-diphosphate; CMP, 5'-cytidylic acid; FAD, flavin adenine dinucleotide; GDP, guanosine 5'-diphosphate; GMP, 5'-guanylic acid; HFCS, high-fructose corn syrup; IMP, 5'-inosinic acid; NAD, nicotinamide adenine dinucleotide; NADP, nicotinamide adenine dinucleotide phosphate; PRPP, 5-phosphoribosyl 1-pyrophosphate; TPP, thiamine pyrophosphate; UDP, uridine 5'-diphosphate; UMP, 5'-uridylic acid.

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Xylitol, which previously was derived from D-xylose by chemical reduction, is used as an energy source for diabetic patients (Mellinghoff, 1961). Recently, a process for the efficient production of xylitol from D-xylose was developed, using a mutant strain of *Candida tropicalis* (Gong, Chen and Tsao, 1981).

D-Xylose and D-xylulose available from vegetable matter have been investigated as potential feedstocks for ethanol production by yeasts (Gong *et al.*, 1981a; Jeffries, 1983; McCracken and Gong, 1983). The conversion of D-xylose to D-xylulose is also being studied because D-xylulose is a better carbon source than D-xylose for yeasts (Wang, Shopsis and Schneider, 1980; Gong *et al.*, 1981b).

This review describes investigations into the microbial production of aldopentoses, ketopentoses, pentitols, aldopentonic acids and some rare derivatives, with particular emphasis on the production of D-ribose, which is the most industrially important pentose.

Naturally occurring pentoses

Pentoses and their derivatives occur widely in various organisms (*Table 1*). The major pentoses, D-ribose, D-xylose and L-arabinose, are most abundant as components of biopolymers. There is a remarkable difference between D-ribose and the other two aldopentoses, in the forms in which they are found: D-ribose and its 2-deoxy derivative, 2-deoxy-D-ribose, are mainly components of the nucleic acids, DNA and RNA, which are concerned with heredity, genetic function and protein synthesis, whereas D-xylose and L-arabinose exist mainly in plant-cell walls as components of the hemicelluloses xylan and arabinan, respectively.

Aldopentoses also exist in compounds other than those described above. D-Ribose occurs in organisms as a component of nucleotide coenzymes such as NAD, NADP, FAD, ADP, UDP, CDP and GDP, as well as in various nucleoside antibiotics. D-Ribose is also present in the cell walls of some bacteria as a component of lipopolysaccharide or of polysaccharide (*Table 1*). 3-Deoxy-D-ribose is a component of the antibiotic cordycepin produced by *Cordyceps militaris* (*Table 1*). 3-Amino-3-deoxy-D-ribose is a component of the antibiotics 3'-amino-3'-deoxyadenosine and puromycin produced by *Streptomyces alboniger* (*Table 1*). With regard to the phosphate derivatives, D-ribose 5-phosphate is an intermediate in the pentose phosphate pathway, and D-ribose 1-phosphate and 5-phosphoribosyl 1-pyrophosphate take part in purine and pyrimidine nucleotide biosynthesis (*see Figures 1 and 3*). Ribitol (adonitol), the reduction product, was first isolated from *Adonis vernalis* (Ranunculaceae) and subsequently was found in the roots of *Bupleurum falcatum*, in pneumococci as a capsular polysaccharide, and in the cell walls of various bacteria as a component of ribitol teichoic acid and of lipopolysaccharide (*Table 1*); it is also a component of riboflavin. The oxidation product, D-riburonic acid, is found in the cell-wall polysaccharides of *Rhizobium meliloti*. 5-Methylthioribose is a component of 5'-methylthioadenosine which has an important role in the metabolism of adenosylmethionine (*Table 1*). Recently, the conversion of 5-methylthioribose to methionine by yeast cells (Shapiro and Schlenk, 1980), by cell-free extracts of *Enterobacter aerogenes* (Shapiro and Barrett, 1981), by

cell-free homogenates of rat liver (Backlund and Smith, 1981) and by apple tissues (Yung, Yang and Schlenk, 1982) has been described.

L-Arabinose is a component of cherry gum and of gum arabic; 4-amino-4-deoxy-L-arabinose has been found in the cell walls of various bacteria as a component of lipopolysaccharide; 2,4-diamino-2,4-dideoxy-L-arabinose is also a component of the antibiotic, prumycin, produced by *Streptomyces* sp. No. 1028; D-xylose is found in cherry gum and in the antibiotic butirosin A produced by *Bacillus circulans* (Table 1).

Apart from these ubiquitous aldopentoses there are others which occur more rarely: D-arabinose is found in bacterial-cell walls as a component of lipid A, lipopolysaccharide or polysaccharide and is also found in the antibiotic, primycin produced by *Streptomyces primycini*; a derivative of L-xylose, 3-O-methyl-L-xylose, is found in the cell wall of *Pseudomonas maltophilia* and *Rhodopseudomonas viridis*, while 3-O-methyl-D-xylose is found in the cell wall of *Myxococcus fulvus*, as a component of lipopolysaccharide; L-lyxose is a component of the antibiotic, curamycin produced by *Streptomyces cura-coi* (Table 1).

All the four ketopentoses and their phosphates are metabolic intermediates in the assimilation of aldopentoses and their reduced derivatives (pentitols) in micro-organisms (Figure 1). In particular, D-ribulose 5-phosphate and D-xylulose 5-phosphate, together with D-ribose 5-phosphate, are major intermediates of the pentose phosphate pathway (Figures 1 and 3). D-Ribulose and D-xylulose are also components of ribulose-peptide in egg yolk, human follicular fluid and human seminal fluid, and of lipopolysaccharide of *Pseudomonas diminuta*, respectively. D-Xylulose and L-xylulose are themselves also intermediates of the uronic acid cycle (Touster and Shaw, 1962), and L-xylulose is found in pentosuric urine (Table 1). L-Ribulose 5-phosphate and L-xylulose 5-phosphate are intermediates in the metabolism of L-arabinose, L-xylose, L-lyxose, ribitol and L-arabinitol (Figure 1). A rare derivative of D-xylulose, 1-deoxy-D-threo-pentulose (1-deoxy-D-xylulose) has been described as an antibiotic produced by *Streptomyces hygroscopicus* (Table 1). This compound has also been postulated as a precursor of the thiazole moiety of thiamine biosynthesis in *Escherichia coli* (Thérisod, Fischer and Estramareix, 1981).

Pentitols (reduction products of aldopentoses) are also naturally occurring: ribitol, as described above, is a derivative of D-ribose; D-arabinitol has been found in *Fistulina hepatica* and subsequently in various lichens (Table 1).

The metabolism of pentoses and their derivatives in micro-organisms is shown in Figure 1. Many enzymes involved in pentose metabolism are used for the production of various pentoses and their derivatives, as described in the following sections.

Production of aldopentoses

D-RIBOSE

Hydrolysis of nucleosides

It should be possible to produce D-ribose and its derivatives from compounds related to the nucleic acids, by using the hydrolytic enzymes found in

Table 1. Natural occurrence of pentoses and their derivatives

Pentose or derivative	Source	Reference
D-Ribose	RNA Nucleotide coenzymes Nucleoside antibiotics Lipopolysaccharide of <i>Salmonella typhimurium</i> Polysaccharide of <i>Eubacterium saburreum</i>	Kauffman <i>et al.</i> , 1962 Hofstad and Lygre, 1977; Hoffman <i>et al.</i> , 1977
2-Deoxy-D-ribose	DNA	Bentley, Cunningham and Spring, 1951
3-Deoxy-D-ribose	Cordycepin (from <i>Cordyceps militaris</i>)	Waller <i>et al.</i> , 1953
3-Amino-3-deoxy-D-ribose	Purromycin (from <i>Streptomyces alboniger</i>) 3'-Amino-3'-deoxyadenosine	Gerber and Lechevalier, 1962; Guarino and Kredich, 1963
Ribitol	<i>Adonis vernalis</i> <i>Bupleurum falcatum</i> Ribitol teichoic acid of Gram-positive bacteria Polysaccharide of <i>Pneumococcus</i> sp.	Wessely and Wang, 1938 Ward, 1981 Rebers and Heidelberger, 1959, 1961; Roberts, Buchanan and Baddiley, 1963 Gmeiner <i>et al.</i> , 1977; Gmeiner, 1977 Miyano <i>et al.</i> , 1983
D-Riburonic acid	Lipopolysaccharide of <i>Proteus mirabilis</i>	
5-Methylthioribose	Lipopolysaccharide of <i>Vibrio parahaemolyticus</i> Riboflavin	
D-Xylose	Polysaccharide of <i>Rhizobium meliloti</i> 5'-Methylthioadenosine Xylan Cherry gum Butirosin A (from <i>Bacillus circulans</i>) Lipopolysaccharide of cell wall of <i>Myxococcus fulvus</i>	Amemura <i>et al.</i> , 1981 Schlenk and Smith, 1953 Jones, 1939, 1947 Dion <i>et al.</i> , 1972 Weckesser <i>et al.</i> , 1971

3-O-Methyl-1-xylose	Lipopolysaccharide of <i>Pseudomonas maltophilia</i> Lipopolysaccharide of <i>Rhodopseudomonas viridis</i>	Brown, Neal and Wilkinson, 1977 Weckesser <i>et al.</i> , 1971, 1974
1-Arabinose	Arabinan Cherry gum Gum arabic	Jones, 1939, 1947 Smith, 1939
4-Amino-4-deoxy-1-arabinose	Lipopolysaccharide of <i>Salmonella</i> spp. Lipid A of <i>Chromobacterium violaceum</i> Lipid A of <i>Rhodospirillum tenue</i> Lipid A of <i>Salmonella</i> spp. Lipid A of <i>Salmonella minnesota</i> Lipid A of <i>Proteus mirabilis</i>	Volk, Galanos and Luderitz, 1970 Hase and Rietschel, 1977 Tharanathan, Weckesser and Mayer, 1977, 1978 Mühlradt, Wray and Lehmann, 1977 Battley, Packer and Redmond, 1982 Sidorczyk, Zähringer and Rietschel, 1983 Ômura <i>et al.</i> , 1974
2,4-Diamino-2,4-dideoxy-1-arabinose	Prumycin (from <i>Streptomyces</i> sp.)	Ômura <i>et al.</i> , 1974
D-Arabinose	Lipid A of <i>Rhodospirillum tenue</i>	Tharanathan, Weckesser and Mayer 1977, 1978; Weckesser <i>et al.</i> , 1977
D-Arabinitol	Lipopolysaccharide of <i>Pseudomonas maltophilia</i> Polysaccharide of <i>Mycobacterium tuberculosis</i> Polysaccharide of <i>Corynebacterium diptheriae</i> Prumycin (from <i>Streptomyces primumi</i>) <i>Fistulina hepatica</i> Lichens	Wilkinson, Galbraith and Anderson, 1983 Chargaff and Anderson, 1930; Maxim, 1930; Haworth, Kent and Stacey, 1948a, b Holdsworth, 1952; Cummins, 1956 Aberhart <i>et al.</i> , 1970 Frèrejacque, 1939 Lindberg, Misiorny and Wachtmeister, 1953; Briner, Grcam and Riggs, 1960; Aghoramurthy, Sarma and Seshadri, 1961
1-Lyxose	Curamycin (from <i>Streptomyces cura-coi</i>)	Galmarini and Deulofeu, 1961
D-Ribulose	Ribulose-peptide of chick yolk Ribulose-peptide of human follicular fluid Ribulose-peptide of human seminal fluid	Amano, 1970 Hayashi, 1971 Nagaoka, 1973
D-Xylulose	Lipopolysaccharide of <i>Pseudomonas diminuta</i>	Wilkinson, 1981
1-Xylulose	Urine of patients with pentosuria	
1-Deoxy-D-threo-pentulose (1-deoxy-D-xylulose)	Antibiotic produced by <i>Streptomyces hygrosopicus</i>	Slechte and Johnson, 1976; Hoeksema and Baczynskyj, 1976

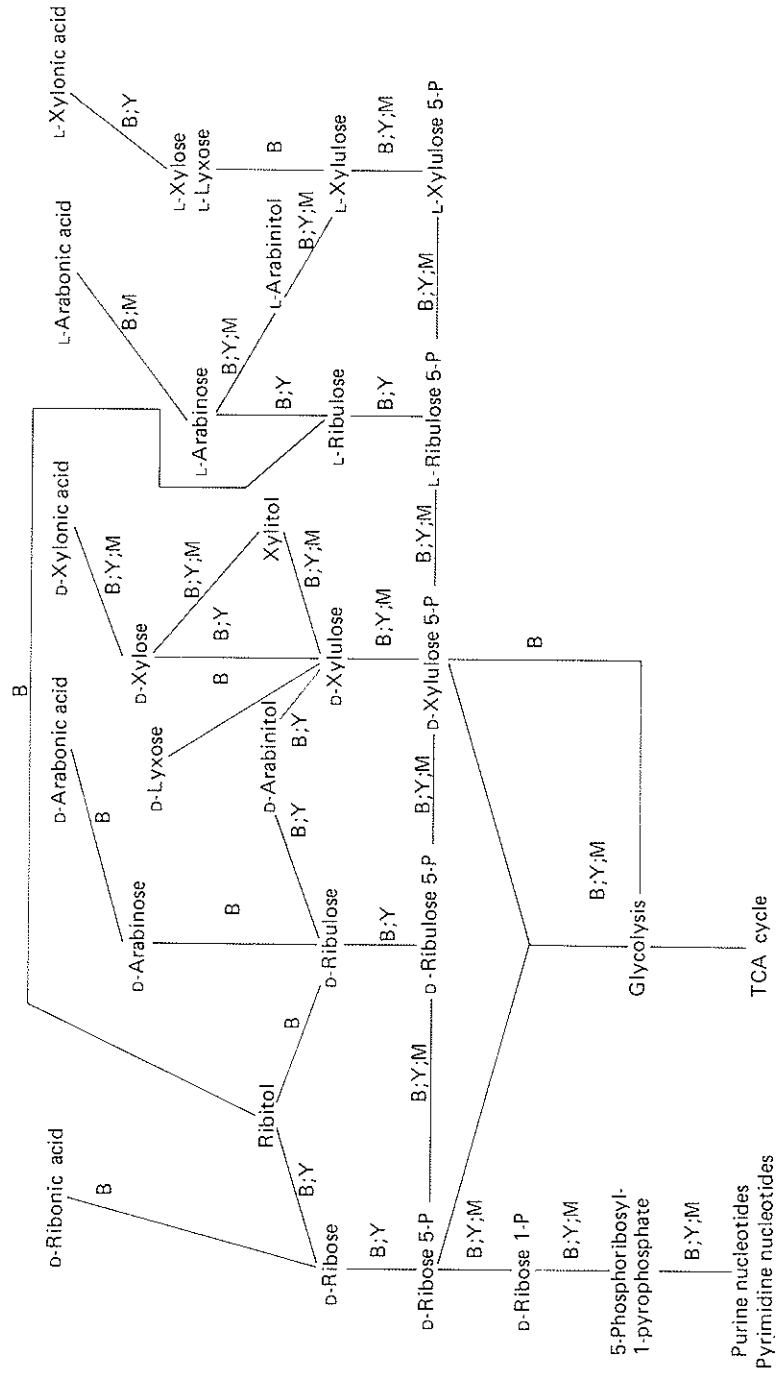
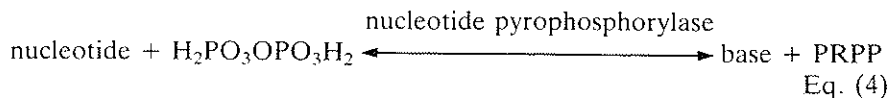
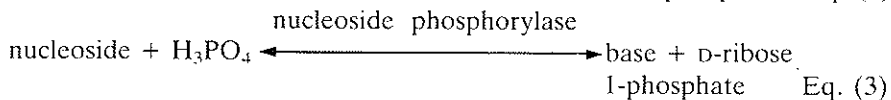
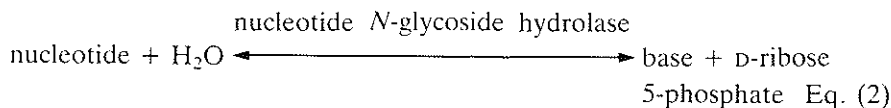
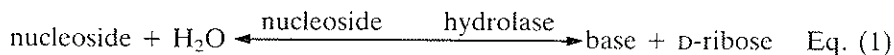


Figure 1. Metabolic pathways of pentoses and their derivatives in micro-organisms. B, bacteria; Y, yeasts; M, moulds.

micro-organisms. The discovery that DNA is the entity that bears genes (Avery, MacLeod and McCarty, 1944; Hershey and Chase, 1952; Watson and Crick, 1953) stimulated many investigations into the mechanism of genetic expression, during which, many enzymes involved in the metabolism of nucleic acids were found, including nucleoside hydrolases (e.g. purine nucleosidase, EC 3.2.2.1; uridine nucleosidase, EC 3.2.2.3, *N*-ribosylpyrimidine ribohydrolyase, EC 3.2.2.8), nucleotide *N*-glycoside hydrolases (e.g. AMP nucleosidase, EC 3.2.2.4; pyrimidine-5'-nucleotide nucleosidase, EC 3.2.2.10), nucleoside phosphorylases and nucleotide pyrophosphorylases. In addition, investigations into the production of the flavour enhancers, inosine monophosphate (IMP) and guanosine monophosphate (GMP), by enzymatic degradation of yeast RNA, started in Japan in the late 1950s (Ogata, 1976); during the course of these investigations, nucleoside hydrolases, nucleotide *N*-glycoside hydrolases and nucleoside phosphorylases were also found in various bacteria, actinomycetes and moulds.

The successful production of IMP and GMP from yeast RNA on an industrial scale gives rise to large amounts of the by-products uridine monophosphate (UMP) and cytidine monophosphate (CMP). D-Ribose, D-ribose 5-phosphate, D-ribose 1-phosphate and 5-phosphoribosyl 1-pyrophosphate (PRPP) can be produced from ribonucleosides and ribonucleotides by hydrolysis with nucleoside hydrolases and nucleotide *N*-glycoside hydrolases, by phosphorolysis with nucleoside phosphorylases and by pyrophosphorolysis with nucleotide pyrophosphorylases, as shown in equations 1-4:



The formulae of D-ribose and its derivatives are shown in *Figure 2*.

The nucleoside hydrolases and nucleotide *N*-glycoside hydrolases found in bacteria, actinomycetes and moulds are listed in *Table 2*. The nucleoside phosphorylases have been reviewed by Imada (1970) and the reverse reaction of equation 4, in which nucleotides are formed from PRPP and bases, has been described by Flaks (1963). D-Ribose production from 5-amino-4-imidazolecarboxamide-riboside by hydrolysis with a nucleoside hydrolase from *Bacillus thiaminolyticus* has been reported (Sano, Yokozeki and Mitsugi, 1977a). The utilization of UMP as the basis of D-ribose 5-phosphate production has also been described (Sakai, Watanabe and Chibata, 1971); UMP was hydrolysed by the nucleotide phosphoribohydrolyase of *Pseudomonas oleovorans*.

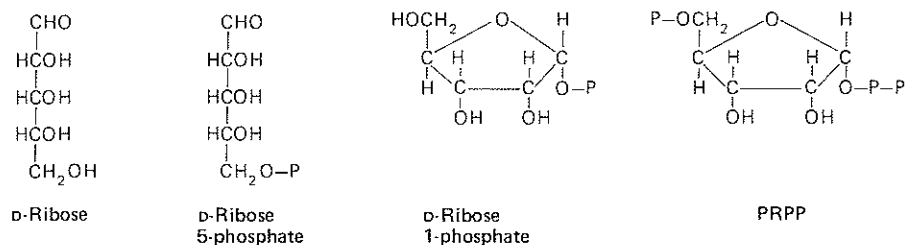


Figure 2. Formulae of D-ribose, D-ribose 5-phosphate, D-ribose 1-phosphate and PRPP.

Table 2. Nucleoside hydrolases and nucleotide *N*-glycoside hydrolases in various micro-organisms

Enzyme	Micro-organism	Reference
Nucleoside hydrolases (e.g. purine nucleosidase, EC 3.2.2.1; uridine nucleosidase, EC 3.2.2.3; <i>N</i> -ribosyl-pyrimidine ribohydrolase, EC 3.2.2.8)	(Bacterium)	
	<i>Bacillus cereus</i> spores	Lawrence, 1955; Powell and Hunter, 1956
	<i>Bacillus thiaminolyticus</i>	Sano, Yokozeki and Mitsugi, 1977a, b
	<i>Lactobacillus delbrueckii</i>	Takagi and Horecker, 1957
	<i>Lactobacillus pentostus</i>	Lampen and Wang, 1952
	<i>Pseudomonas fluorescens</i>	Terada, Tatibana and Hayaishi, 1967
	<i>Xanthomonas phaseoli</i>	Hochster and Nozzolillo, 1961
Nucleotide <i>N</i> -glycoside hydrolases (e.g. AMP nucleosidase, EC 3.2.2.4; pyrimidine-5'-nucleotide nucleosidase, EC 3.2.2.10)	(Yeast)	
	Baker's yeast	Heppel and Hilmoe, 1952
	Fleishman's yeast	Carter, 1951
	(Bacterium)	
	<i>Azotobacter vinelandii</i>	Hurwitz, Heppel and Horecker, 1957
	<i>Pseudomonas graveolens</i>	Imada <i>et al.</i> , 1963
	<i>Pseudomonas oleovorans</i>	Sakai, Watanabe and Chibata, 1968, 1971
(Actinomycetes)		
<i>Streptomyces virginiae</i>	Imada, Kuno and Igarashi, 1967	
(Mould)		
<i>Aspergillus oryzae</i>	Kuninaka, 1956, 1957, 1959	

Production and accumulation in the culture medium by wild-type micro-organisms

The accumulation of small amounts of D-ribose was first observed in culture media of *Penicillium brevi-compactum* (Simonart and Godin, 1951) during studies on the biosynthesis of components of benzene derivatives in *P. brevi-compactum* (Godin, 1953a,b). An unidentified bacterium was later found to excrete both D-ribose and D-ribose 5-phosphate into the culture medium (Suzuki *et al.*, 1963). When the culture medium contained Mn^{2+} , Fe^{2+} or Zn^{2+} ions, D-ribose (5 mg/ml) accumulated; however, if these ions were not

present, D-ribose 5-phosphate accumulated instead, in concentrations of up to 7 mg/ml. A smaller degree of D-ribose accumulation was also described by Saito and Sugiyama (1966), working with *Pseudomonas reptilivora*.

D-Ribose production by transketolase-deficient Bacillus spp. mutants

Mutant strains of bacteria, which have various blocks in their metabolic pathways, have been used for the production of many metabolic intermediates that are useful chemicals, such as amino acids and substances related to nucleic acids. A microbial method for the industrial production of D-ribose was first brought about by the isolation and development of transketolase-deficient mutants of *Bacillus* spp. (Sasajima and Yoneda, 1971).

During research into the production of inosine (one of the precursor substances for IMP synthesis) (Nogami *et al.*, 1968) attempts were made to isolate *Bacillus* spp. mutants that were defective in the pentose phosphate pathway, in order to improve inosine productivity (Sasajima, Nogami and Yoneda, 1970), as D-ribose 5-phosphate is a precursor of purine nucleotide biosynthesis. However, inosine productivity of certain of these mutants unexpectedly decreased, whereas it was found that large amounts of pentoses were excreted into the culture medium. These mutants were found to be deficient in transketolase or in D-ribulose 5-phosphate 3-epimerase (ribulosephosphate 3-epimerase; EC 5.1.3.1) (Sasajima and Yoneda, 1974). The transketolase-deficient (*tkt*) mutants produced only D-ribose, whereas the epimerase-deficient mutant produced both D-ribose and D-ribulose simultaneously in the ratio of about 2:1. D-Ribose was purified, isolated by crystallization and identified by its chemical and physicochemical properties. The *tkt* mutants were found among those which were isolated as strains requiring shikimic acid, because transketolase also catalyses the first step of the aromatic biosynthetic pathway; thus, the *tkt* mutant is defective both in the pentose phosphate pathway and in the aromatic biosynthetic pathway (Figure 3). The mutant strain therefore cannot assimilate carbohydrates such as D-gluconate, D-xylose and L-arabinose and, moreover, requires aromatic compounds such as L-tryptophan, L-phenylalanine, L-tyrosine, coenzyme Q, vitamin K and folic acid (Sasajima and Yoneda, 1974). Revertants could not produce D-ribose, indicating that the production of a large amount of D-ribose is directly related to the transketolase deficiency.

D-Glucose, sorbitol, D-mannitol and maltose are good carbon sources for D-ribose production, and yeast extract is an excellent nitrogen source.

The *tkt* mutant was modified by further mutation to obtain improved strains, the best of which produced about 70 mg of D-ribose per ml of culture medium (Sasajima, 1976). Figure 4 shows a typical time course for D-ribose production by fermentation. Derepressed synthesis of a spore-specific enzyme, D-glucose dehydrogenase (EC 1.1.1.119) was shown by the vegetative cells of this improved mutant strain (Yokota, Sasajima and Yoneda, 1979; Yokota and Sasajima, 1981). Synthesis of D-glucose dehydrogenase usually starts at stage III of sporulation, in parallel with the morphological changes attendant on spore formation (Warren, 1968). The initiation of sporulation

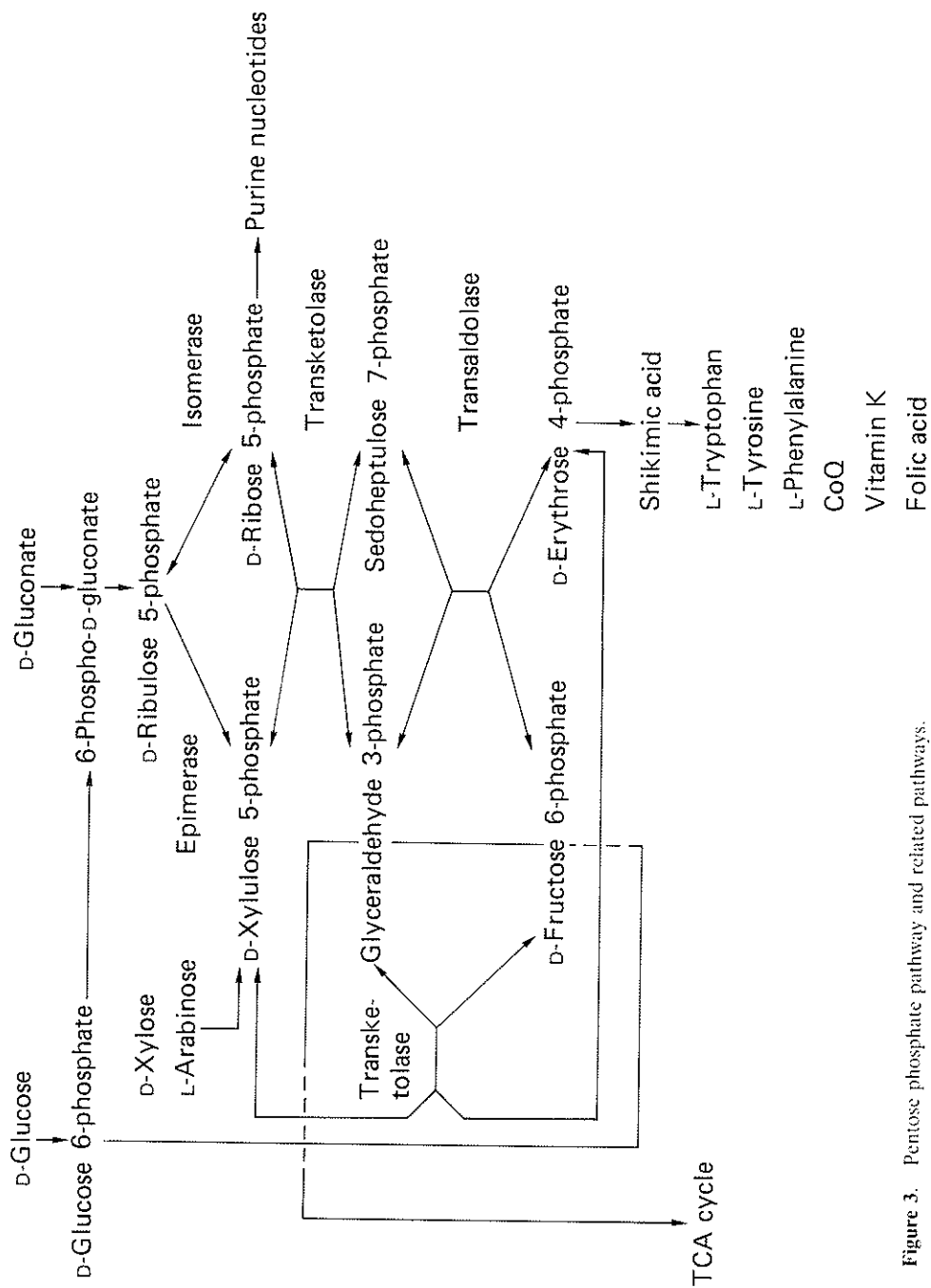


Figure 3. Pentose phosphate pathway and related pathways.

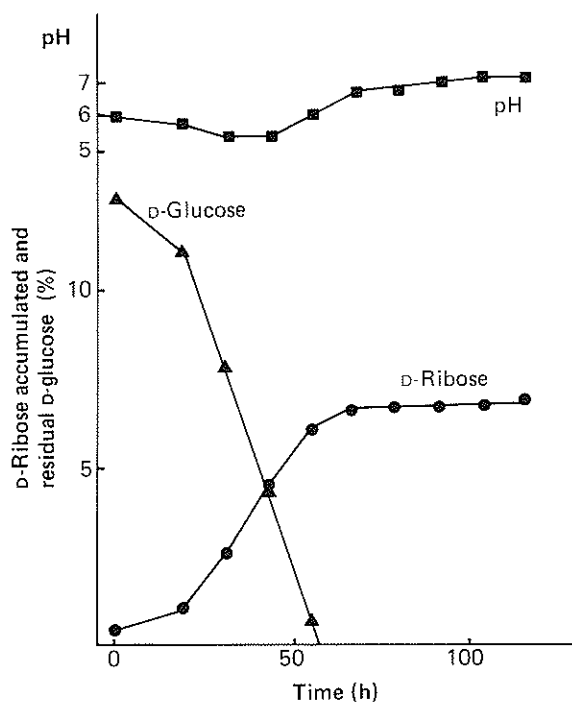


Figure 4. Time course of D-ribose production.

normally occurs only after depletion of the carbon source or of another essential nutrient. However, in the improved *tkt* mutant strain, synthesis of D-glucose dehydrogenase occurs even in the presence of D-glucose and is not associated with the morphological changes of sporulation (Yokota, Sasajima and Yoneda, 1979; Yokota and Sasajima, 1981). In the mutant strain, both the non-phosphorylated pathway (from D-glucose to the pentose phosphates via D-gluconate) and the phosphorylated pathway are active (Figure 5). The gluconate pathway may contribute greatly to the high productivity of the improved strain. The ratio of D-ribose and D-gluconate production depends on the oxygen partial pressure during fermentation (K. Sasajima and co-workers, unpublished work); oxygen deficiency leads to D-gluconate rather than D-ribose accumulation. Further improvement of D-ribose production was achieved by another mutation which rendered the improved mutant strain asporogenous (Sasajima, 1976) but the mechanism of this effect has not been elucidated.

The kinetics of D-ribose production by the high-yielding mutant strain was studied by Asai *et al.* (1978) who showed that the ratio of D-ribose to D-gluconate production was influenced by temperature, the maximum yield of D-ribose being noted at 36.6°C when using exponential growth cells as the inoculum.

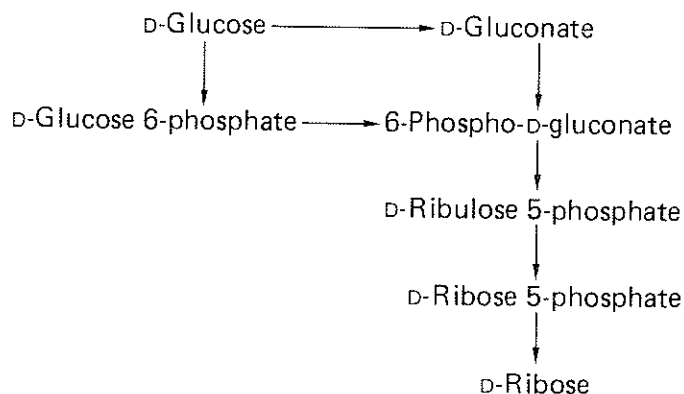


Figure 5. Pathways of D-ribose formation.

A mutant strain of this type has been used over the past decade for production of D-ribose (for riboflavin synthesis) on an industrial scale. Almost all of the world's D-ribose production is now thought to be by the microbial process.

Transketolase and D-ribulose 5-phosphate 3-epimerase mutants of the IFO 3026 strain of *Bacillus subtilis* were subsequently isolated and found also to produce pentoses (Sasajima, 1976). These mutants produced both D-ribose and D-ribulose. The transketolase mutant of another strain of *B. subtilis*, IFO 12114, also formed a pentose, in this case D-ribose only (A. Yokota and K. Sasajima, unpublished work). Because transketolase is one of the enzymes requiring thiamine pyrophosphate (TPP) as a cofactor, thiamine-requiring mutants of *B. subtilis* IFO 12114 were then isolated. These could produce D-ribose when grown in a thiamine-depleted medium but, even so, yields were less than with the *tkt* mutant, probably because the thiamine levels could not be decreased sufficiently to eliminate transketolase activity without adversely affecting the activity of certain enzymes (such as the pyruvate dehydrogenase complex (EC 1.2.4.1) and α -ketoglutarate dehydrogenase (oxoglutarate dehydrogenase; EC 1.2.4.2)) for which TPP is required.

A pleiotropic effect was noted in the transketolase mutant in that it could not utilize D-glucose, which normally is the best carbon source for D-ribose production (Sasajima and Yoneda, 1974; Sasajima, Kumada and Yokota, 1977). The mutant strain preferentially used other substances in the medium as a carbon and energy source and for growth, and only later was able to use D-glucose for D-ribose production. Investigation showed that the transport function of the $\text{EnzII}^{\text{glc}}$ (phosphohistidinoprotein - hexose phosphotransferase; EC 2.7.1.69) of the PEP-dependent D-glucose phosphotransferase system (Postma and Roseman, 1976; Saier, 1977) was defective in the *tkt* mutant (Sasajima and Kumada, 1979). Utilization of D-mannitol, D-fructose and glycerol, but not of sorbitol, was inhibited by D-glucose. The *tkt* mutant was found to be hypersensitive to D-glucose repression of synthesis of the enzymes

of D-mannitol catabolism (such as D-mannitol 1-phosphate dehydrogenase, EC 1.1.1.17 and the D-mannitol transport system). On the other hand, the *tkt* mutant was resistant to D-glucose repression of synthesis of enzymes of sorbitol catabolism, (such as the sorbitol transport system and sorbitol dehydrogenase (Sasajima and Kumada, 1981a). D-Gluconate, D-xylose and L-arabinose were also found to repress the synthesis of enzymes of D-mannitol catabolism in the *tkt* mutant, although not in the parental strain. These changes in the regulation of enzyme synthesis may be caused by a defect in the cell membrane of the *tkt* mutant. Subsequently, various functions relating to the cell surface were found to differ from those of the parental strain: (1) during the exponential growth phase the *tkt* mutant formed chains which were thicker in cell width than those of the parental strain; (2) sensitivity to bacteriophages SP10 and SP01 was altered; (3) the cell walls of the mutant strain autolysed more slowly than did those of the parental strain; (4) the sporulation frequency of the mutant strain decreased markedly (Sasajima and Kumada, 1981b, 1983a). The flagellae are also defective in the mutant strain, which is therefore non-motile (Sasajima and Kumada, 1983b). Isolation and characterization of a true revertant confirmed that these pleiotropic properties were generated by a single mutation (Sasajima and Kumada, 1979, 1981a, 1983a,b). Chemical changes in the membrane components are being investigated.

Tkt mutants of *Escherichia coli* and *Salmonella typhimurium* have also been isolated (Josephson and Fraenkel, 1969; Eidels and Osborn, 1971). The *tkt* mutants of *E. coli* did not accumulate any pentose, either intracellularly or extracellularly (Josephson and Fraenkel, 1974); accumulation of pentoses was not studied in the *S. typhimurium tkt* mutants. The *tkt* mutants of these Gram-negative bacteria also showed defective synthesis of heptose which is important in the biosynthesis of the outer-membrane lipopolysaccharides, resulting in the formation of a defective cell surface (Eidels and Osborn, 1971; Ames, Spudich and Nikaido, 1974; Koplów and Goldfine, 1974; Bayer, Koplów and Goldfine, 1975; Irvin *et al.*, 1975; Smit, Kamio and Nikaido, 1975; van Alphen, Lugtenberg and Berendsen, 1976). The difference in D-ribose productivity between the *tkt* mutants of *E. coli* and those of *Bacillus* spp. may result from their different genetic backgrounds.

D-XYLOSE AND L-ARABINOSE

These two aldopentoses occur in plant-cell walls as the hemicelluloses xylan and arabinan, and can comprise a large proportion of plant biomass. As a consequence there is interest in the conversion of xylan and arabinan to D-xylose and L-arabinose respectively (Figure 6), and subsequent conversion of these pentoses to valuable products such as ethanol and single-cell protein; the utilization of D-xylose has recently been reviewed (Gong *et al.*, 1981a; Jeffries, 1983; McCracken and Gong, 1983).

Hemicelluloses can be hydrolysed either by a chemical process using dilute sulphuric acid, or by an enzymatic method using hemicellulases; chemical hydrolysis is now the more usual technique (Jeffries, 1983). In the enzymatic

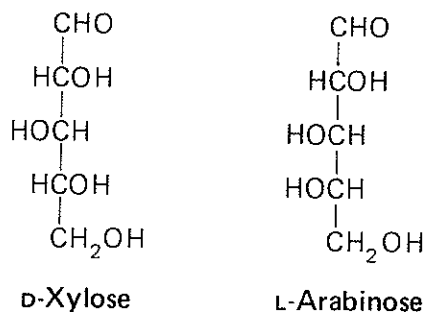


Figure 6. Formulac of D-xylose and L-arabinose.

process a complex enzyme mixture must be used because hemicelluloses comprise various sugar components with different types of chemical bonds. Investigations from 1950 to 1973 on the occurrence, purification, properties and mode of action of the hemicellulases, including the xylan- and arabinan-degrading enzymes, have been reviewed (Dekker and Richards, 1976). *Table 3* summarizes studies since 1974 on enzymes from micro-organisms, including xylanases (EC 3.2.1.8), β -xylosidases (exo-1,4- β -D-xylosidase, EC 3.2.1.37), endo-1,5- α -L-arabinases (EC 3.2.1.99), exo-type arabinases and α -L-arabinofuranosidases (EC 3.2.1.55).

Acid hydrolysates of the hemicelluloses are much more difficult for micro-organisms to utilize, probably because of the formation of furfural and other inhibitory by-products. Hemicellulases therefore could become of value for the large-scale production of D-xylose and L-arabinose from biomass if their production and use could be made more economic. Studies on cloning genes encoding these enzymes (*see* page 198) may offer promise, together with isolation of constitutive mutants for production of these enzymes, because xylan and arabinan are required to induce xylanases and arabinases, respectively (Takenishi and Tsujisaka, 1975; Johnson *et al.*, 1979; Esteban, Villanueva and Villa, 1982; Kaji, Sato and Tsutsui, 1981).

Production of ketopentoses

OXIDATION OF PENTITOLS

The oxidation of polyols to ketoses by polyol dehydrogenases of acetic acid bacteria is a well-known reaction; the oxidation of sorbitol to sorbose by acetic-acid bacteria has been used by the pharmaceutical industry in the production of vitamin C. Pentitols are also oxidized by acetic-acid bacteria to ketopentoses. Ribitol and D-arabinitol were first found to be oxidized to L-ribulose and D-xylulose (*Figure 7*), respectively, by polyol dehydrogenases of

Table 3. Xylanases, β -xylosidases, arabinases and α -L-arabinofuranosidases in various micro-organisms

Enzyme	Micro-organism	Reference
Xylanase (EC 3.2.1.8)	(Bacterium)	
	<i>Bacillus circulans</i>	Johnson <i>et al.</i> , 1979; Esteban, Villanueva and Villa, 1982
	<i>Bacillus subtilis</i>	Bernier <i>et al.</i> , 1983
	<i>Bacillus</i> sp.	Uchino and Nakane, 1981; Williams and Withers, 1983
	(Actinomycetes)	
	<i>Streptomyces</i> sp.	Nakanishi, Yasui and Kobayashi, 1976
	(Yeast)	
	<i>Schizophyllum commune</i>	Paice <i>et al.</i> , 1978
	(Mould)	
	<i>Aspergillus niger</i>	Takenishi and Tsujisaka, 1975
<i>Gliocladium virens</i>	Takahashi and Kutsumi, 1979	
<i>Malbranchea pulchella</i> var. <i>sulfurea</i>	Matsuo, Yasui and Kobayashi, 1975	
Basidiomycetes	Kubačková, Karácsonyi and Váradi, 1975	
β -Xylosidase (EC 3.2.1.37)	(Bacterium)	
	<i>Bacillus pumilus</i>	Clayssens <i>et al.</i> , 1975
	<i>Bacillus</i> spp.	Williams and Withers, 1983
	(Mould)	
Basidiomycetes	Kubačková, Karácsonyi and Váradi, 1975	
<i>Malbranchea pulchella</i> var. <i>sulfurea</i>	Matsuo, Yasui and Kobayashi, 1977a, b	
Endo-1, 5- α -L-arabinase (EC 3.2.1.99)	(Bacterium)	
	<i>Bacillus subtilis</i>	Kaji and Saheki, 1975
Exo-type arabinase	(Bacterium)	
	<i>Erwinia carotovora</i>	Williams and Withers, 1983
α -L-Arabinofuranosidase (EC 3.2.1.55)	(Bacterium)	
	<i>Erwinia carotovora</i>	Kaji and Shimokawa, 1984
	(Bacterium)	
	<i>Bacillus subtilis</i>	Yoshihara and Kaji, 1983
	<i>Bacillus</i> spp.	Williams and Withers, 1983
	(Actinomycetes)	
	<i>Streptomyces diastatochromogenes</i>	Higashi <i>et al.</i> , 1983
	<i>Streptomyces purpurascens</i>	Komae, Kaji and Sato, 1982
<i>Streptomyces</i> sp.	Kaji, Sato and Tsutsui, 1981; Kusakabe, Yasui and Kobayashi, 1975	
(Yeast)		
<i>Rhodotorula flava</i>	Kusakabe, Yasui and Kobayashi, 1975	
(Mould)		
<i>Aspergillus niger</i>	Kusakabe, Yasui and Kobayashi, 1975	

Acetobacter suboxidans (Reichstein, 1934; Prince and Reichstein, 1937). Table 4 lists the pentitol dehydrogenases found in various micro-organisms.

Moses and Ferrier (1962) described the use of cell suspensions of *Acetobacter suboxidans* in the preparation of D-xylulose and L-ribulose from D-arabinitol and ribitol, respectively. Subsequently, ribitol dehydrogenase (EC 1.1.1.56) and D-arabinitol dehydrogenase (EC 1.1.1.11) of *Aerobacter aerogenes* were

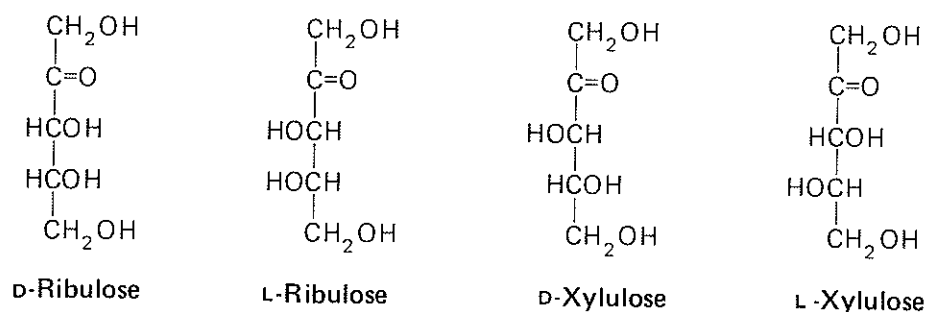


Figure 7. Formulae of ketopentoses.

Table 4. Pentitol dehydrogenases in various micro-organisms

Enzyme	Micro-organism	Reference
Pentitol dehydrogenases (and non-specific polyol dehydrogenases)	(Bacterium) <i>Acetobacter suboxidans</i>	Reichstein, 1934; Prince and Reichstein, 1937; Hann, Tilden and Hudson, 1938; Arcus and Edson, 1956; Moses and Ferrier, 1962
	<i>Azotobacter agilis</i>	Marcus and Marr, 1961
	<i>Pseudomonas</i> spp.	Stanier, Palleroni and Doudoroff, 1966
	(Yeast) <i>Candida utilis</i>	Arcus and Edson, 1956
	<i>Pichia miso</i>	Ōnishi and Saito, 1962
Xylitol dehydrogenase (D-xylulose reductase, EC 1.1.1.9)	Various yeasts	Barnett, 1968
	(Bacterium) <i>Rhizobium trifolii</i>	Primrose and Ronson, 1980
	(Yeast) <i>Candida utilis</i>	Chakravorty <i>et al.</i> , 1962; Horitsu and Tomocda, 1966
	(Mould) <i>Penicillium chrysogenum</i>	Chiang and Knight, 1960b
Ribitol dehydrogenase (EC 1.1.1.56)	Various moulds and yeasts	Chiang and Knight, 1960a
	(Bacterium) <i>Aerobacter aerogenes</i>	Wood, McDonough and Jacobs, 1961; Mortlock and Wood, 1964; Mortlock, Fossitt and Wood, 1965; Mortlock <i>et al.</i> , 1965
D-Arabinitol dehydrogenase (EC 1.1.1.11)	<i>Escherichia coli</i>	Scangos and Reiner, 1978
	<i>Rhizobium trifolii</i>	Primrose and Ronson, 1980
	(Bacterium) <i>Aerobacter aerogenes</i>	Wood, McDonough and Jacobs, 1961; Lin, 1961; Mortlock and Wood, 1964; Mortlock, Fossitt and Wood, 1965; Mortlock <i>et al.</i> , 1965
	<i>Escherichia coli</i> <i>Rhizobium trifolii</i>	Scangos and Reiner, 1978 Primrose and Ronson, 1980

utilized to prepare D-ribulose from ribitol and L-xylulose from L-arabinitol, and D-xylulose from D-arabinitol, respectively (Mortlock and Wood, 1966). The particular pentulose produced from ribitol was found to vary according to the origin of the pentitol dehydrogenases employed.

A cell suspension of an *Aerobacter aerogenes* mutant that was ribitol dehydrogenase-constitutive and D-ribulokinase (EC 2.7.1.47)-deficient was most effective in the formation of D-ribulose (Oliver *et al.*, 1969). In the parental strain, the D-ribulose that was formed was further metabolized and assimilated.

ISOMERIZATION OF ALDOPENTOSEs

During investigations into the pentose phosphate pathway in the early 1950s, pentose isomerases were found in various bacteria. Cohen (1953) noted the conversion of D-ribulose to D-arabinose by the D-arabinose isomerase (EC 5.3.1.3) of *Escherichia coli* and then the formation of D-xylulose from D-xylose by D-xylose isomerase (EC 5.3.1.5) of *Lactobacillus pentosus*, *Pseudomonas hydrophila* and *Pasteurella pestis* was described. Studies on other isomerases (D- and L-arabinose, D-xylose and D-lyxose isomerases) in other bacteria have been reported (Table 5). Subsequent investigations revealed that D-arabinose isomerase might be identical to L-fucose isomerase (Green and Cohen, 1956; Camyre and Mortlock, 1965; Oliver and Mortlock, 1971; Izumori and Yamanaka, 1974), because D-arabinose is a rare pentose (Table 1). L-Arabinose isomerases (EC 5.3.1.4), which catalyse the initial reaction of L-arabinose assimilation, have also been found in various bacteria (Table 5).

The D-xylose isomerase of *Pseudomonas hydrophila* was found to catalyse interconversion between D-glucose and D-fructose (Marshall and Kooi, 1957) and therefore has been intensively studied for practical use in the production of D-fructose from D-glucose (Chen, 1980a,b). Glucose isomerases (essentially D-xylose isomerases) were found in various micro-organisms and some are now used for the industrial production of high-fructose corn syrup (HFCS) (Chen, 1980a, b; see also Harada (1984) and Poulsen (1984) in volume 1 of this Series).

D-Lyxose ketol-isomerase (EC 5.3.1.15) has been found in *Aerobacter aerogenes* (Table 5). Both L-xylose and L-lyxose can be isomerized into L-xylulose by L-fucose isomerase (Anderson and Wood, 1962; Mortlock, Fossitt and Wood, 1965).

D-Ribose is unusual in its catabolism as well as in its mode of occurrence. Other aldopentoses may be reduced to pentitols by reductases or isomerized to ketopentoses by isomerases (Figure 1): D-ribose, however, is first phosphorylated by ribokinase (EC 2.7.1.15) before transformation. Thus a strictly defined D-ribose isomerase has not yet been identified, but an isomerase (L-rhamnose isomerase, EC 5.3.1.14), which acts not only on L-rhamnose but also on D-ribose and L-lyxose and is induced by any one of these sugars, was found in *Mycobacterium smegmatis* (Izumori, Rees and Elbein, 1975; Izumori, Yamanaka and Elbein, 1976; Izumori, Mitchell and Elbein, 1976) and will convert D-ribose into D-ribulose.

D-Xylose isomerase and L-arabinose isomerase have been found in *Candida*

Table 5. Pentose isomerases in various micro-organisms

Enzyme	Micro-organism	Reference
D-Arabinose isomerase (EC 5.3.1.3)	(Bacterium) <i>Aerobacter aerogenes</i>	Mortlock and Wood, 1964; Camy myre and Mortlock, 1965; Oliver and Mortlock, 1971; Izumori and Yamanaka, 1974
	<i>Escherichia coli</i>	Cohen, 1953; Green and Cohen, 1956
	<i>Mycobacterium smegmatis</i>	Izumori, Yamanaka and Elbein, 1976
L-Arabinose isomerase (EC 5.3.1.4)	(Bacterium) <i>Aerobacter aerogenes</i>	Simpson, Wolin and Wood, 1958
	<i>Escherichia coli</i>	Lee and Englesberg, 1962
	<i>Lactobacillus gayonii</i>	Yamanaka, 1962
	<i>Lactobacillus plantarum</i>	Heath <i>et al.</i> , 1958
	<i>Lactobacillus</i> spp.	Yamanaka, 1958
	<i>Mycobacterium smegmatis</i>	Izumori, Yamanaka and Elbein, 1976; Izumori, Ueda and Yamanaka, 1978
	(Yeast) <i>Candida utilis</i>	Horitsu, Sasaki and Tomoyeda, 1970
D-Xylose isomerase (EC 5.3.1.5)	(Bacterium) <i>Aerobacter aerogenes</i>	Natake and Yoshimura, 1963
	<i>Aerobacter cloacae</i>	Tsumura and Sato, 1960, 1961a,b, 1965a
	<i>Bacillus coagulans</i>	Yoshimura, Danno and Natake, 1966; Danno, 1970, 1971
	<i>Bacillus megaterium</i>	Takasaki and Tanabe, 1962a,b
	<i>Brevibacterium pentoso- aminoacidicum</i>	Ichimura <i>et al.</i> , 1965
	<i>Escherichia coli</i>	David and Wiesmeyer, 1970
	<i>Escherichia intermedia</i>	Natake and Yoshimura, 1964a,b
	<i>Flavobacterium arborescens</i>	Boguslawski, 1983
	<i>Lactobacillus brevis</i>	Yamanaka, 1963a,b
	<i>Lactobacillus gayonii</i>	Yamanaka, 1962
	<i>Lactobacillus pentosus</i>	Mitsuhashi and Lampen, 1953
	<i>Lactobacillus xylosus</i>	Yamanaka and Takahara, 1977
	<i>Lactobacillus</i> spp.	Yamanaka, 1958
	<i>Pasteurella pestis</i>	Slein, 1955
	<i>Pseudomonas hydrophila</i>	Hochster and Watson, 1953, 1954
	<i>Salmonella typhimurium</i>	Mortlock and Old, 1979; Sha- manna and Sanderson, 1979a
	(Actinomycetes) <i>Actinoplanes missouriensis</i>	Scallet <i>et al.</i> , 1974
	<i>Streptomyces albus</i>	Sanchez and Smiley, 1975
	<i>Streptomyces flavogriseus</i>	Chen, Anderson and Han, 1979
	<i>Streptomyces griseus</i>	Giovenco, Morisi and Pansolli, 1973
<i>Streptomyces phaeochro- mogenes</i>	Tsumura and Sato, 1965b; Strandberg and Smiley, 1971	
<i>Streptomyces</i> sp.	Takasaki, 1966; Takasaki, Kosugi and Kanbayashi, 1969; Chou, Ladisch and Tsao, 1976	
(Yeast) <i>Candida utilis</i>	Tomoyeda and Horitsu, 1964	
<i>Rhodotorula gracilis</i>	Höfer, Betz and Kotyk, 1971	
D-Lyxose ketol- isomerase (EC 5.3.1.15)	(Bacterium) <i>Aerobacter aerogenes</i>	Anderson and Allison, 1965

utilis and *Rhodotorula gracilis*, and in *Candida utilis*, respectively (Table 5) although pentose isomerases are not commonly found in fungi because, in these species, aldopentoses are normally metabolized by reduction to pentitols which are then oxidized to ketopentoses (Chiang and Knight, 1960b).

Because D-xylulose was found to be more efficiently converted to ethanol by yeasts than was D-xylose (Wang, Shopsis and Schneider, 1980; Gong *et al.*, 1981b), the conversion of D-xylose to D-xylulose has been studied by, for instance, the use of immobilized whole cells of *Bacillus* spp. (Chiang *et al.*, 1981). *Fusarium oxysporum* f.sp. *lini* and *Aspergillus niger* have been used to consume D-xylose in the preisomerized mixture of D-xylose and D-xylulose to provide a purified D-xylulose solution. In another instance, borate was added to the reaction mixture to push the isomerization equilibrium point towards D-xylulose (Hsiao *et al.*, 1982). Wang, Johnson and Schneider (1980) and Gong *et al.* (1981b) added D-xylose isomerase directly to the fermentation medium to produce ethanol via D-xylulose from D-xylose.

ACCUMULATION IN THE CULTURE MEDIUM

Saito and Sugiyama (1964) first reported the accumulation (up to 1.3 mg/ml) of a ketopentose in the culture medium of *Brevibacterium fuscum*. Subsequently, non-tumorigenic strains of *Agrobacterium tumefaciens* were found to accumulate D-ribulose in the culture medium, whereas the tumorigenic strains produced relatively little D-ribulose (Suzuki and Hochster, 1965). Both D-ribulose and D-xylulose were found (7–8 mg/ml) in the culture medium of several *Brevibacterium* and *Corynebacterium* spp. (Misawa, Nara and Kinoshita, 1967). Shimamura, Yoshitake and Imai (1971) noted the formation of up to 9.5 mg of D-ribulose per ml, by a thiamine-requiring *Corynebacterium* sp. in a thiamine-deficient medium containing 6% D-gluconate as the carbon source. Investigation showed that the D-ribulose accumulation resulted from the decreased transketolase activity in media containing low levels of thiamine (Shimamura, Yoshitake and Imai, 1973). The derived D-ribulose 5-phosphate 3-epimerase mutant of *Bacillus* spp. accumulated both D-ribose and D-ribulose in the culture medium, in an approximate ratio of 2:1 (Sasajima and Yoneda, 1971). The total pentose yield was 40 mg per ml of the culture medium.

Production of pentitols

Production of D-arabinitol (Figure 8) by yeasts was first suggested by Binkley and Wolfrom (1950). Subsequently, during the course of studies on glycerol production, it was found that D-arabinitol was produced from D-glucose together with glycerol by osmophilic yeasts (Table 6). D-Arabinitol was the main product under conditions of nitrogen restriction (Spencer and Sallans, 1956; Ōnishi, Saito and Koshiyama, 1961; Hajny, 1964), high sugar concentration (Ōnishi, 1960a; Moran and Witter, 1979) or low inorganic phosphate concentration (Peterson, Hendershot and Hajny, 1958). Low pH also stimulated D-arabinitol production by *Moniliella tomentosa* (Hanssen, van Regenmortel and Verachtert, 1972), *Candida lipolytica* (Tabuchi and Hara, 1973) and *Candida tropicalis* (Hattori and Suzuki, 1974a).

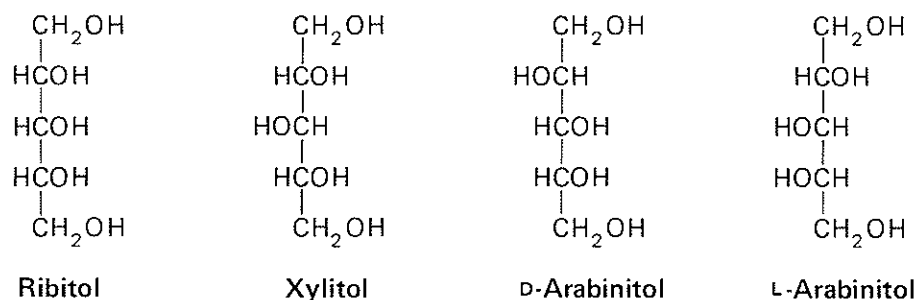


Figure 8. Formulae of pentitols.

Table 6. Yeasts producing D-arabinitol from D-glucose and *n*-alkane

Yeast	Reference
(From D-glucose)	
Fermentation residue	Binkley and Wolfrom, 1950
<i>Candida lipolytica</i>	Tabuchi and Hara, 1973
<i>Candida tropicalis</i>	Hattori and Suzuki, 1974a
<i>Debaryomyces subglobosus</i>	Anderson and Harris, 1963
<i>Endomycopsis chodati</i>	Hajny, 1964
<i>Hansenula arabitoligenes</i>	Chang, Wang and Yang, 1963; Chang, Yang and Wang, 1963
<i>Moniliella tomentosa</i>	Hanssen, van Regenmortel and Verachtert, 1972
<i>Pichia miso</i>	Ōnishi, Saito and Koshiyama, 1961
<i>Saccharomyces rouxii</i>	Spencer, Roxburgh and Sallans, 1957; Ōnishi, 1960a; Moran and Witter, 1979
<i>Zygosaccharomyces chevalieri</i>	Chang, Wang and Yang, 1963
<i>Zygosaccharomyces</i> spp.	Peterson, Hendershot and Hajny, 1958
<i>Zygosaccharomyces</i> spp. and other osmophilic yeasts	Spencer and Sallans, 1956
Various yeasts	Ōnishi, 1960b
(From <i>n</i> -alkane)	
<i>Candida tropicalis</i>	Hattori and Suzuki, 1974a
<i>Candida zeylanoides</i>	Hattori and Suzuki, 1974b

Investigation into the useful conversion of petroleum products revealed that *Candida tropicalis* and *Candida zeylanoides* produced D-arabinitol from *n*-alkanes at low pH (Table 6).

The production of pentitols from aldopentoses by bacteria and yeasts has also been investigated (Table 7). Ōnishi and Perry (1965) first found that *Pichia miso* produced xylitol (Figure 8) and heptitols from D-xylose, while Ōnishi and Suzuki (1966) reported that *Candida polymorpha* produced xylitol from D-xylose, L-arabinitol (Figure 8) from L-arabinose and ribitol (Figure 8) from D-ribose in a yield of 30–40% of sugars consumed. *Pichia quercuum* was reported simultaneously to produce both xylitol (the reduced product) and D-xylonic acid (the oxidized product) from D-xylose (Suzuki and Ōnishi, 1967,

Table 7. Micro-organisms reducing aldopentoses to pentitols

Micro-organism	Reference
(Bacterium)	
<i>Corynebacterium</i> sp.	Yoshitake <i>et al.</i> , 1971; Yoshitake, Shimamura and Imai, 1973, 1976
<i>Enterobacter liquifaciens</i>	Yoshitake <i>et al.</i> , 1973, 1976
(Yeast)	
<i>Candida polymorpha</i>	Ōnishi and Suzuki, 1966
<i>Candida tropicalis</i> mutant	Gong, Chen and Tsao, 1981
<i>Pichia quercuum</i>	Suzuki and Ōnishi, 1967, 1973

1973). Some bacterial strains also produced pentitols from aldopentoses (Table 7). A *Corynebacterium* sp. produced xylitol from D-xylose, L-arabinitol from L-arabinose and ribitol from D-ribose using D-gluconate as the energy and carbon source (Yoshitake *et al.*, 1971; Yoshitake, Shimamura and Imai, 1973, 1976). *Enterobacter liquifaciens* was shown to produce xylitol in culture media containing only D-xylose as the sole carbon source (Yoshitake *et al.*, 1973, 1976). A mutant strain of *Candida tropicalis* has been reported to produce xylitol from D-xylose in a very high yield (Gong, Chen and Tsao, 1981).

Xylitol has been prepared from D-glucose in a three-stage process: (1) D-arabinitol was produced from D-glucose by *Debaryomyces hansenii*; (2) D-arabinitol was then converted to D-xylulose by *Acetobacter suboxidans*; (3) finally, D-xylulose was reduced to xylitol by *Candida guilliermondii* (Ōnishi and Suzuki, 1969).

Production of aldopentonic acids

Various micro-organisms have been reported to oxidize aldopentoses to the corresponding aldopentonic acids, the formulae of which are shown in Figure 9. Bertrand (1898a,b) first demonstrated the formation of xylonic acid from xylose and of arabonic acid from arabinose by *Acetobacter xylinum*: subsequently the production of aldopentonic acids from aldopentoses by numerous

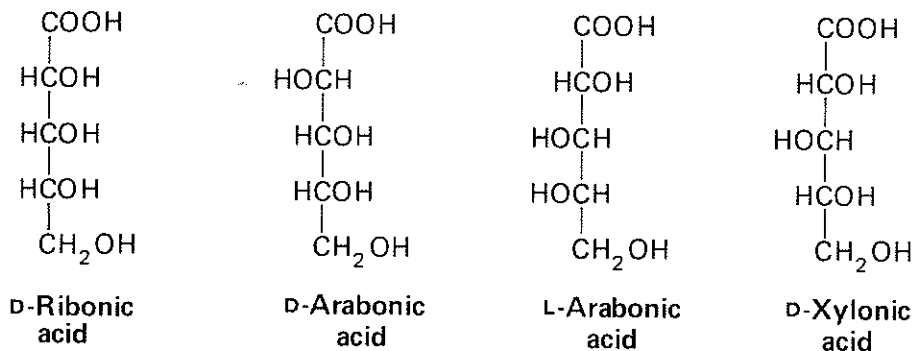


Figure 9. Formulae of aldopentonic acids.

Table 8. Micro-organisms oxidizing aldopentoses to aldopentonic acids

Pentose oxidized*	Micro-organism	Reference
D-Xylose→D-xylic acid	(Bacterium)	
	<i>Acetobacter melanogenum</i>	Bernhauer and Riedl-Třimovř, 1950
	<i>Acetobacter suboxidans</i>	Bernhauer and Riedl-Třimovř, 1950
	<i>Acetobacter xylinum</i>	Bertrand, 1898a
	<i>Aerobacter aerogenes</i>	Masuo and Nozaki, 1956
	<i>Erwinia milletiae</i>	Uchida and Suzuki, 1975
	<i>Micrococcus</i> sp.	Ohsugi, Tochikura and Ogata, 1970
	<i>Pseudomonas fragi</i>	Weimberg, 1961
	<i>Pseudomonas</i> spp.	Lockwood and Nelson, 1946
	(Yeast)	
	<i>Pichia quercuum</i>	Suzuki and Ōnishi, 1967, 1973
	<i>Pullularia pullulans</i>	KieSSLing, Lindberg and McKay, 1962
	L-Arabinose→L-arabonic acid	(Mould)
<i>Fusarium lini</i>		Hayashida, 1938
<i>Penicillium corylophilum</i>		Ikeda and Yamada, 1963a,b
(Bacterium)		
<i>Acetobacter melanogenum</i>		Bernhauer and Riedl-Třimovř, 1950
D-Arabinose→D-arabonic acid	<i>Acetobacter suboxidans</i>	Bernhauer and Riedl-Třimovř, 1950
	<i>Acetobacter xylinum</i>	Bertrand, 1898b
	<i>Aerobacter aerogenes</i>	Masuo and Nozaki, 1956
	<i>Erwinia milletiae</i>	Uchida and Suzuki, 1975
	<i>Pseudomonas fragi</i>	Weimberg, 1961
	<i>Pseudomonas saccharophila</i>	Weimberg and Doudoroff, 1955
	<i>Pseudomonas</i> spp.	Lockwood and Nelson, 1946
	(Mould)	
	<i>Fusarium lini</i>	Hayashida, 1938
	(Bacterium)	
	<i>Pseudomonas fragi</i>	Weimberg, 1961
	<i>Pseudomonas riboflavina</i>	Foster, 1944
	<i>Pseudomonas saccharophila</i>	Palleroni and Doudoroff, 1957
<i>Pseudomonas</i> spp.	Lockwood and Nelson, 1946	
D-Ribose→D-ribonic acid	(Bacterium)	
	<i>Pseudomonas fragi</i>	Weimberg, 1961
	<i>Pseudomonas riboflavina</i>	Foster, 1944
	<i>Pseudomonas</i> spp.	Lockwood and Nelson, 1946

* Detailed enzyme studies were not reported in the literature cited. For details of aldopentose dehydrogenases see Table 9.

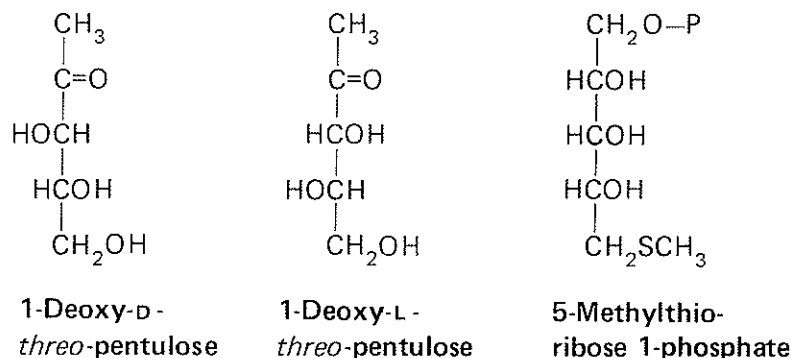
micro-organisms was described, as listed in Table 8. The enzymes (aldopentose dehydrogenases and oxidases) which catalyse these reactions, have also been characterized and are listed in Table 9.

Production of rare derivative sugars of pentoses

The accumulation of 1-deoxy-D-*threo*-pentulose (Figure 10) by *Streptomyces hygrosopicus* has been described (Slecht and Johnson, 1976; Hoeksema and Baczynskyj, 1976). During the course of studies on D-ribose production by the *tkt* mutants of *Bacillus* spp., it was found that the *tkt* mutant of *Bacillus pumilus* formed a new monosaccharide, 1-deoxy-D-*altro*-heptulose (Yokota, Sasajima

Table 9. Aldopentose dehydrogenases in various micro-organisms

Enzyme	Micro-organism	Reference
D-Xylose oxidase (un-purified)	(Yeast) <i>Phellinus igniarius</i> <i>Trametes versicolor</i>	Lyr, 1962 Lyr, 1962
D-Xylose dehydrogenase (EC 1.1.1.175)	(Bacterium) <i>Arthrobacter</i> sp.	Yamanaka, Kaneda and Sakai, 1977; Yamanaka, Gino and Kaneda, 1977
L-Xylose dehydrogenase (EC 1.1.1.113)	(Yeast) Baker's yeast	Uehara and Takeda, 1962
L-Arabinose dehydrogenase (EC 1.1.1.46)	(Bacterium) <i>Rhizobium japonicum</i> <i>Rhizobium</i> spp.	Pedrosa and Zancan, 1974 Duncan, 1979
D-Arabinose dehydrogenase (EC 1.1.1.117)	(Bacterium) <i>Pseudomonas</i> sp.	Hu and Cline, 1964; Cline and Hu, 1965; Dahms and Anderson, 1969
D-threo-Aldose dehydrogenase	(Bacterium) <i>Pseudomonas caryophylli</i>	Sasajima and Sinskey, 1979

**Figure 10.** Formulae of 1-deoxy-D-threo-pentulose, 1-deoxy-L-threo-pentulose and 5-methylthioribose 1-phosphate.

and Horii, 1978). Further studies on the mechanism of the heptulose formation (Yokota and Sasajima, 1983) revealed that 1-deoxy-D-threo-pentulose and 1-deoxy-L-threo-pentulose (Figure 10) were also formed from acetoin, methylacetoin or pyruvate plus D- or L-glyceraldehyde, respectively, by the cell-free extracts of the mutant strain (Yokota and Sasajima, 1984). 1-Deoxy-D-threo-pentulose has been reported to be a precursor of the thiazole moiety of thiamine biosynthesis in *Escherichia coli* (Th  risod, Fischer and Estramareix, 1981). Investigation of the origin of 1-deoxy-D-threo-pentulose and 1-deoxy-L-threo-pentulose in various micro-organisms demonstrated the presence in them of enzymes synthesizing the deoxy-pentuloses (Yokota and Sasajima, 1984).

Another unusual pentose derivative, 5-methylthioribose 1-phosphate (Figure 10) was produced from 5'-methylthioadenosine by a phosphorylase (Ferro, Wrobel and Nicolette, 1979).

Gene manipulation in pentose production

The isolation and utilization of mutants with blocked carbohydrate-metabolism pathways has been found to be of great value for the production of D-ribose, D-ribulose and xylitol. Gene manipulations such as DNA recombination and cell fusion now promise new methods to improve pentose-production processes. These techniques will improve yields and formation of microbial enzymes essential for the economic production of pentoses and their derivatives. Although industrial applications have not yet been achieved, the following notes indicate some of the topics which are now being intensively investigated.

Cloning of DNA fragments encoding D-xylose isomerase has been achieved in *Escherichia coli* (Maleszka, Wang and Schneider, 1982; Polaina *et al.*, 1982; Wovcha, Steuerwald and Brooks, 1983; Ohira, Takahashi and Saito, 1983) and in *Salmonella typhimurium* (Ghangas and Wilson, 1984). The activity of D-xylose isomerase of *E. coli* was amplified fivefold by employing the recombinant plasmid pUC1002 (Wovcha, Steuerwald and Brooks, 1983). D-Xylose isomerase activity of *S. typhimurium* carrying the plasmid pGG22 was one and a half times that of the wild-type strain (Ghangas and Wilson, 1984). The D-xylose operon is situated at the 78–79 min site of chromosomes of both *E. coli* (Maleszka, Wang and Schneider, 1982; Bachmann, 1983) and *S. typhimurium* (Shamanna and Sanderson, 1979b; Sanderson and Roth, 1983). Attempts are being made to construct a plasmid carrying the D-xylose isomerase gene and permitting expression in yeast (Ohira, Takahashi and Saito, 1983). If successful, this work could contribute to the economic production of ethanol from D-xylose.

Cloning of xylanase and β -xylosidase genes could contribute to the hydrolysis of xylan to D-xylose by xylan-degrading enzymes and could assist the utilization of plant biomass. In fact, genes encoding the xylanase and β -xylosidase of *Bacillus pumilus* have already been cloned and expressed in *Escherichia coli* (Panbangred *et al.*, 1983; Shinmyo *et al.*, 1983). One of the isolated plasmids, pOXN29R, expressed in *E. coli* β -xylosidase activity seven to eight times that shown in *B. pumilus*. Construction of a hybrid plasmid which carries the xylanase gene and expresses its activity in *B. subtilis* has also been reported, although the full paper has not yet appeared in the literature (Panbangred, Shinmyo and Okada, 1983; Shinmyo *et al.*, 1983): *B. subtilis* with the hybrid plasmid had xylanase activity which was two- to threefold that of *B. pumilus*. In this instance, xylanase was excreted into the culture medium, whereas expression of the gene in *E. coli* was limited to the cytoplasm. The xylanase gene of *Bacillus subtilis* was also cloned and expressed in *E. coli* (Bernier, Driguez and Desrochers, 1983). The intracellular xylanase produced by the transformed *E. coli* strain was purified and found to have an activity equivalent to one-quarter of the extracellular production by *B. subtilis*.

A hybrid plasmid, carrying genes for xylanase, β -xylosidase and D-xylose isomerase, and capable of expression in *Saccharomyces cerevisiae*, is envisaged because of its potential value in the production of ethanol from xylan.

Conclusions

The production of D-ribose, D-xylose, D-xylulose and xylitol are all of practical importance: D-ribose provides material for riboflavin synthesis; D-xylose and D-xylulose are intermediates in the utilization of xylan from biomass; xylitol is used in the treatment of diabetic patients.

Interest in pentose production on an industrial scale is now centred on D-ribose production for the synthesis of riboflavin for use in pharmaceuticals and as an animal-feed additive. The isolation and utilization of mutant strains, notably the transketolase-deficient mutant of *Bacillus* spp., which has been improved by further mutation, is being used in microbial processes of D-ribose production which are now replacing chemical methods. Mutants blocked in certain metabolic pathways have also been obtained for efficient production of D-ribulose and xylitol.

Future work involving genetic engineering techniques such as DNA recombination and cell fusion will help to develop and to improve processes for the production of pentoses as well as other useful compounds.

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