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PENTOSE-FERMENTING YEASTS IN NATURE: ECOLOGY, BIODIVERSITY, AND APPLICATIONS

The world's energy sector has undergone drastic changes in the last decades due to the climate change and the turn to renewable energy sources. Biomass is the largest renewable source of carbohydrates on the Earth and is an important substrate for biofuel production. Saccharomyces cerevisiae yeasts are the main producer of first-generation ethanol from corn and sugarcane. However, these yeasts lack the ability to utilize the important components of lignocelluloses such as pentoses D-xylose and L-arabinose. Pentose-fermenting yeasts could become an alternative to S. cerevisiae in ethanol production from lignocelluloses. This review focuses on the ecology, geographical distribution, taxonomy, and potential applications of naturally-occurring pentose-fermenting yeasts. Pentose-fermenting yeasts have been frequently found in the lignocellulose-associated substrates. Decaying and rotten wood and the gut of wood-boring insects are especially important natural reservoirs of this group of yeasts. Simple sugars xylose and L-arabinose would be present in such habitats as suitable nutrients for pentose-assimilating yeasts. The other natural habitats reported for pentose-fermenting yeasts are soil, plants, and herbivore faeces. Pentose-fermenting yeasts are found in many geographical regions and have been isolated on almost each continent. Dozens of novel pentose-fermenting yeast species have been discovered in the last decade. The previously poorly explored regions, including Brazil, China, and several Asian countries were especially often reported as sites of isolation of such yeasts. Most xylose-fermenting yeasts belong to genera Scheffersomyces, Candida, Spathaspora, Sugiyamaella, and Pachysolen, while the most efficient ethanol producers are represented by species Scheffersomyces stipitis and Spathaspora passalidarum. The vast majority of research on the biotechnological application of pentose-fermenting yeasts focuses on their role in the production of bioethanol from lignocellulose. This group of yeasts could be either directly involved in the fermentation stage of ethanol production or serve as a source of genetic material for the genetic manipulation of other industrial yeast strains. Pentose-fermenting yeasts could also be involved in the production of various chemicals from lignocellulosic substrates, mainly polyols, xylitol, and arabitol. Thus, the search for novel pentose-fermenting yeasts that could become new efficient ethanol producers or donors of new genetic material is still ongoing. The previously unexplored or poorly studied geographical regions and natural habitats can hide many novel yeasts with huge biotechnological potential.

Keywords: *yeasts, pentose fermentation, ecology, application of yeasts*

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In the last decades, the world experienced a drastic turn from conventional fuels like gas and petroleum to renewable sources of energy (solar energy, wind, and biomass). The production of biofuels is only one of the several possible ways to mitigate the harm from conventional sources of energy and develop new sustainable processes of energy generation [1]. USA and Brazil were both the pioneers in the wide-scale production of the first-generation bioethanol that originated from starch- and sugar-rich substrates, i.e. corn and sugarcane. However, the use of such food substrates for energy production is controversial due to the competition over farmlands and the increase in food prices [2].

Plant biomass is the most abundant renewable source of carbohydrates on the Earth and consists of three major components: cellulose, hemicelluloses, and lignin. Cellulose is the major constituent of lignocellulose consisting of D-glucose monomers joined by β-1,4-glycosidic bonds. Cellulose is characterized by high crystallinity and is fairly difficult to degrade [3]. The second main component of plant biomass is hemicelluloses, which are heteropolymers of hexoses (glucose, mannose, and galactose), pentoses (xylose and L-arabinose), and uronic acids. Hemicellulose is more susceptible to hydrolysis compared to the other lignocellulose components. Lignin is a non-carbohydrate phenolic polymer and is the most undegradable component of plant biomass [4].

The most commonly used microorganism for bioethanol production is yeast *S. cerevisiae*. It is characterized by high ethanol yields, tolerance to many stress factors, and GRAS status. However, *S. cerevisiae* lack the ability to assimilate and ferment pentoses (xylose and L-arabinose), which make up a large proportion of lignocellulose sugars [5]. Search for an efficient yeast strain capable to ferment both pentoses and hexoses and withstand the harsh conditions of industrial ethanol production has been going on over several decades [6].

There are currently two main ways to achieve such a purpose. Both have their own advantages and drawbacks. First, the search for suitable candidates has been conducted in nature, especially in ecological niches rich in lignocellulosic substrates [6]. Another way to develop an efficient producer is by genetic engineering either the naturally-occurring pentose-fermenting yeasts or constructing *S. cerevisiae* strains with pentose-fermenting abilities [7]. There are several excellent reviews on the recent advances in genetic engineering strategies to improve the efficiency of ethanol production from lignocellulose by yeasts and to increase strain robustness [6—8].

The scope of this review is ecology, geographical distribution, taxonomy, and potential industrial application of naturally occurring pentose-fermenting yeasts.

Natural habitats and geographical distribution of pentose-fermenting yeasts. Early works on pentose-assimilating or pentose-fermenting yeasts were performed by screening large national or university collections. In 1976, the majority of the known yeast species were assessed for the assimilation and fermentation of various carbon sources [9]. None of the surveyed yeasts were found to ferment either D-xylose or L-arabinose, but a high proportion of strains could aerobically assimilate these pentoses.

Toivola et al evaluated xylose-fermenting activity of more than 200 types of yeast strains from Centraalbureau voor Schimmelcultures (CBS), the Netherlands, and discovered six yeast species that produced more than 1 g/L ethanol from 20 g/L xylose: *Brettanomyces naardenensis*, *Candida (Scheffersomyces) shehatae*, *Candida tenuis*, *Pachysolen tannophilus*, *Pichia (Scheffersomyces) segobiensis*, and *Pichia (Scheffersomyces) stipitis* [10]. The authors emphasized on the fact that all the efficient ethanol producers were isolated from lignocellulosic substrates or sources associated with wood. So, in the following years, large screenings for xylose-fermenting yeasts were also carried out among yeasts isolated from

wood-associated niches. A quantitative assessment of ethanol production from xylose was performed by du Preez and Prior for 56 yeast strains isolated from soil in South Africa [11]. *P. stipitis, C. shehatae,* and several *Candida* strains were shown to produce high levels of ethanol.

164 yeast strains isolated from black knots, insect frass, and tree exudates in Canada and 262 yeast strains isolated from cactus fruits and associated with *Drosophila* flies in Bahamas were screened for the xylose fermentation by Nigam et al [12]. Many of the isolates were able to produce ethanol from xylose in negligible amounts. However, only 36 yeast isolates represented by species *Aureobasidium pullulans, Candida famata, Candida guilliermondii, Candida maltosa, Candida parapsilosis, Candida sonorensis,* and *Candida* spp. synthesized more than 1 g/L from 2% xylose.

In the following decades, several large screening surveys for xylanolytic and xylose-fermenting yeasts were carried out in such lignocellulose-based natural habitats as rotten wood and wood-feeding insects. The first study to discover xylose-fermenting yeasts in rotting wood in the Brazilian Amazonian Forest was conducted by Cadete et al [13]. Altogether 224 yeast strains were isolated from 40 samples of rotting wood. 33 different yeast species were found in this study (26 previously known species and 7 novel species); *Candida tropicalis, Vanrija humicola* and *Candida boidinii* being the most frequently isolated yeasts. Two strains of *Sc. stipitis*, seven strains of *Sp. passalidarum,* and several strains of four novel species *Spathaspora* were shown to convert xylose into ethanol with various degrees of efficiency.

In another major study, 321 yeast strains isolated from rotting wood samples from two sites in Brazil were assessed for their ability to ferment xylose and hydrolize xylan [14]. 69 yeast species have been identified in this study, and 15 of them were previously unknown. 14 of 69 detected yeast species produced ethanol from D-xylose, while 20 of 69 yeast species obtained in this work also produced extracellular xylanases.

330 yeast strains from 200 samples of rotting wood in the Brazilian Rain Forest were surveyed for ethanol and xylanase production [15]. *Pichia manshurica, Candida pseudolambica*, and *Wickerhamomyces* sp. were the most frequently isolated yeasts. Altogether, 80 yeast species have been detected, 14 species of these were previously unknown. More than 16% isolates were able to produce ethanol from D-xylose and belonged to 19 known and 6 novel species. The most efficient ethanol producers from xylose belonged to *Sc. stipitis*, *Scheffersomyces* sp. and *Spathaspora boniae.* Also 13% isolates (predominantly *Apioctrichum sporotrichoides, A. pullulans, Saitozyma podzolica,* and *Su. xylanicola*) demonstrated high xylanase activity. In another study, 17 of 105 yeast strains isolated from rotten wood in Central China fermented D-xylose [16] and belonged to *Scheffersomyces* clade (*Sc. insectosa, Sc. lignosus, Sc. segobiensis, Sc. stipitis, Sc. Shehatae,* and *Sp. passalidarum).* A new novel xylose-fermenting yeast species *Sc. henanensis* has been described as well.

The gut of wood-ingesting insects also proved to be a rich natural reservoir for xylose-assimilating and fermenting yeasts. Yeast found in the gut of such insects likely assists their hosts in the hydrolysis of the ingested wood while being able to access easily available sugars [3]. Suh et al reported the frequent detection of *Pichia (Scheffersomyces) stipitis*-like xylose-fermenting yeasts in the gut of wood-boring beetles and made a conclusion regarding a significant symbiotic association between wood-ingesting beetles and xylose-fermenting yeasts [17]. The study of gut microbiota of more than 300 adult beetles and larval *Odontotaenius disjunctus* resulted in the description of new species of xylose-fermenting yeasts *Sp. passalidarum* and *Candida jeffriesii* [18].

The gut of 16 species of wood-boring beetles in Guatemala that live in dead wood proved to be especially rich in yeasts with cellobiose- and xylose-fermenting activities [19]. Altogether, 771 yeast strains belonging to 78 yeast species were isolated. The most commonly isolated yeasts be-

longed to xylose-fermenting species *Sc. shehatae* (314 strains) and *Sc. stipitis* (109 strains). Several undescribed xylose- and cellobiose-fermenting yeast species belonging to *Lodderomyces, Scheffersomyces, Spathaspora,* and *Sugiyamaella* clades have also been found.

92 yeast strains that belonged to 18 yeast species were isolated from the gut of the wood-feeding termite *Reticulitermes chinensis* [20]. Seven novel species *Candida gotoi, Candida pseudorhagii, Hamamotoa lignophila, M. guilliermondii, Sugiyamaella* sp.1, *Sugiyamaella* sp.2, and *Sugiyamaella* sp. 3 were detected. *C. pseudorhagii* were the most commonly isolated yeast species and possessed high xylanase activity and the ability to ferment xylose. More examples of pentose-fermenting yeasts inhabiting the gut of wood-feeding insects are shown in Table 1.

Another interesting natural habitat for xylose-fermenting yeasts was the dung of herbivore mammals (Table 1). 39 xylose-assimilating strains have been isolated from faeces of vari-

Table 1. **Distribution and diversity of pentose-fermenting yeasts in nature**

Isolation source	Description of isolation source and site	Yeast species	Pentose fermented	Reference
Soil	Various soil samples, South Africa	*C. shehatae, P. stipitis*	D-xylose	[11]
	Woodland soil, South Africa	*Candida lyxosophila*	D-xylose	[21]
	Field soil, Japan	*Candida* sp.	D-xylose, L-arabinose	[22]
	Tropical peat, Thailand	*Candida kantuleensis*	D-xylose	[23]
Rotting and dead wood	Rotting wood from Amazonian forest, Brazil	*Sp. passalidarum, Sc. stipitis, Candida amazonensis*	D-xylose	[13]
		Spathaspora brasiliensis, Sp. suhii, Sp. roraimanensis, Sp. xylofermentans	D-xylose	[24]
	Rotting wood from Rain forest, Brazil	*Spathaspora arborariae*	D-xylose	[25]
	Rotting wood from Rain forest, Brazil	*Spathaspora girioi, Spathaspora hagerdaliae, Spathaspora gorwiae*	D-xylose	[26]
	Rotting wood from Rain forest, Brazil	*C. boidinii, C. cellulosicola, C. melibiosica, C. tropicalis, C. intermedia, M. guilliermondii, Sc. queiroziae, Sc. shehatae, Sc. stipitis, S. polymorphus, Su. boreocaroliniensis, W. pijperi*	D-xylose	[14]
	Rotting wood, the Galapagos Archipelago, Ecuador	*Sc. stipitis*	D-xylose	[27]
	Rotten wood, Poland	*Sc. shehatae*	D-xylose	[28]
	Rotten wood, China	*Scheffersomyces insectosa Scheffersomyces lignosus, Sc. segobiensis, Sc. stipitis, Sc. shehatae, Sp. passalidarum*	D-xylose	[16]
	Rotting wood, China	*Sugiyamaella yunanensis*	D-xylose	[29]
	Rotting wood, China	*Scheffersomyces jinghongensis, Scheffersomyces paraergatensis*	D-xylose	[30]
	Rotten wood, Ukraine	*Sc. stipitis*	D-xylose	[31]
Plants and fungi	Rotten fruits, Nigeria	*Pichia kudriavzevii, C. tropicalis*	D-xylose	[32]
	Pepper, tomato and sugarcane bagasse, Brazil	*Galactomyces geotrichum, Candida akabanensis*	D-xylose	[33]
	Black knots on cherry trees, Canada	*A. pullulans, Candida* sp.	D-xylose	[12]

Continuation of Table 1.

Isolation source	Description of isolation source and site	Yeast species	Pentose fermented	Reference
Insects	Gut of silkworm larva *Bombyx mori*, India	*Blastobotrys bombycis*	D-xylose	[34]
	Frass of unidentified wood boring insect larvae from pine and larch trees, USA	*Candida arabinofermentans*	L-arabinose	[35]
	Gut of wood-boring beetles *Odontotaenius disjunctus*, USA	*Sp. passalidarum, C. jeffriesii*	D-xylose	[18]
	Gut of passalid beetles, Guatemala	*Sc. shehatae, Sc. stipitis, Spathaspora* spp., *Scheffersomyces* spp.	D-xylose	[19]
	Gut of wood roach *Cryptocercus* sp., USA	*Scheffersomyces cryptocercus*	D-xylose	[19]
	Gut of wood-feeding termite, *Reticulitermes chinensis*, China	*Candida pseudorhagii, Hamamotoa lignophila, M. guilliermondi, Sugiyamaella* sp.	D-xylose	[20]
	Gut of scarabeid beetle *Allomyrina dichotoma*, China	*Spathaspora allomyrinae*	D-xylose	[36]
	Gut of beetle *Dorcus titanus*, China	*Scheffersomyces titanus*	D-xylose	[37]
	Gut of beetle, *Anoplophora leechi*, China	*Scheffersomyces anoplophorae*	D-xylose	[30]
Mammal faeces	Herbivore faeces, Thailand	*Zygoascus meyerae*	D-xylose	[38]
	Herbivore faeces, South Africa	*Candida xylanilytica, P. kudriavzevii, Ogataea methanolica, C. tropicalis*	D-xylose	[39]

ous herbivores in Thailand. Although several strains converted xylose into ethanol, the efficiency was low, and the highest ethanol yields were observed for *Zygoascus meyerae* strain [38]. Among 101 fungal isolates from the dung of wild herbivores in South Africa, only 36 strains were represented by yeasts [39]. Six yeast strains were able to convert xylose to ethanol, although ethanol yields were very low. As the herbivore diet usually contains lignocellulosic materials, the presence of xylose-utilizing microorganisms in the excretions of these animals is to be expected. However, very few studies on yeast diversity and physiology in such habitats were carried out and ethanologenic strains reported in those works produced low levels of ethanol from xylose.

The search for yeasts capable to ferment pentose L-arabinose, another major constituent of hemicelluloses, produced less promising results. 116 yeast strains maintained in ARS Culture Collection (National Center for Agricultural Utilization Research, USA) were screened for the ability to produce ethanol from L-arabinose [40]. Seven yeast strains *Candida auringiensis, Candida succiphila, Ambrosiozyma monospora*, and *Candida* sp. (NRRL YB-2248) produced detectable amounts of ethanol (up to 4 g/L) after prolonged cultivation. Some of these strains were isolated from trees or tree exudates and insect frass, i.e. wood-based substrates. Strain *Candida* sp. NRRL YB-2248 and the other two strains isolated from insect frass of pine and larch trees were identified as *C. arabinofermentans* on the basis of phylogenetical analysis. They were able to produce 0.7—1.9 g/L ethanol from L-arabinose [35]. In the following years, there were few reports regarding L-arabinose-fermenting yeasts. Watanabe et al. described

L-arabinose-fermenting yeast strain *Candida* sp. NY7122 isolated from field soil in Japan and closely related to *Candida subhashii* [22]. This isolate was capable of fermenting a wide range of hexoses and pentoses D-xylose and L-arabinose. However, the efficiency of pentose conversion to ethanol by this strain was low. A large survey of 390 yeast strains isolated from banana waste, the gut of dung beetles, marula wine, and herbal concoctions in South Africa led to the selection of 13 strains with D-xylose and L-arabinose fermenting activity [41]. The authors were able to improve the most efficient strain *Meyerozyma carribica* through evolutionary engineering. However, the ethanol yields remained too low for efficient industrial exploitation.

In conclusion, despite the extensive search for efficient ethanol producers from L-arabinose in various ecological niches, few L-arabinose-fermenting yeasts have been discovered, and their potential for full-scale ethanol production from lignocellulose is uncertain.

Geographical patterns of distribution of pentose-fermenting yeasts are comparatively hard to define, as large screening programs were performed only in few, predominantly large countries, including USA, China, and Brazil. The first surveys for xylose-fermenting yeasts in nature were done in Canada and South Africa [11, 12]. A large number of strains of xylose-fermenting yeasts *Sc. stipitis* were also isolated from various wood-based substrates in USA and France [42]. One of the well-studied xylose-fermenting yeasts *Sc. stipitis* was found in wood-associated substrates in various geographical locations, including Europe, North, Central America [43], Brazil [13, 14], South Africa [11], China [16], and Ukraine [31]. Its close relative *Sc. shehatae* was also detected in various lignocellulose-based habitats in South Africa [11], China [16], Brazil [14], Guatemala [19], and Poland [28].

Recently, several large studies on yeast biodiversity in various Brazilian ecosystems have resulted in the isolation of many previously known species of xylose-fermenting yeasts belonging to *Scheffersomyces* and *Spathaspora* clades [13, 14]. Also, several novel xylose-fermenting yeast species belonging to the genera *Spathaspora* [13, 25, 26, 43] and *Sugiyamaella* [44] were described (Table 2). A number of known and novel pentose-fermenting yeasts have been detected in Asian region: from the gut of wood-feeding insects [20, 36] and rotten wood in China [16, 29], field soil in Japan [22], rotten fruit and tree bark in India [45], the gut of silkworm in India [34], from moss and tropical peat [23, 46] and herbivore faeces in Thailand [37]. There are several reports on pentose-fermenting yeasts in Africa, mainly from South Africa [11, 21, 39] and Nigeria [32]. It should be noted that vast areas on the continent, especially in tropical and subtropical forests, remain unexplored and could be a rich natural reservoir of L-arabinose and D-xylose-fermenting yeasts.

The discovery of so many novel pentose-fermenting yeast species in previously unexplored regions could indicate the presence of a vast diversity of novel yeasts with valuable biotechnological properties, just waiting to be discovered. The exploration of new geographical regions and perhaps unusual ecological niches could lead to the discovery of microorganisms with biotechnologically relevant enzymes or metabolic traits and mechanisms.

Taxonomy of pentose-fermenting yeasts

The ability to efficiently ferment xylose is a rare characteristic among yeasts that is limited by several related yeast genera. It should be emphasized that a number of yeast species, including several *Candida* and *Pichia* species, are capable to produce small amounts of ethanol from xylose [10]. However, this review is focused on more efficient pentose-fermenting yeasts that are represented by *Candida, Scheffersomyces, Spathaspora,* and *Pachysolen* genera.

The first report on xylose fermentation by yeast *C. tropicalis* was made by Karczewska in 1958 [50]. Since then, dozens of yeasts species

have been reported to be able to ferment D-xylose. The most well-known and studied representative of the xylose-fermenting yeasts is *Sc. stipitis*. There are several reviews on its physiology, genetics, and potential application [7, 51—53], so there will be only a short description of this species in this review. The strains of *Sc. stipitis* probably possess the highest capacity of xylose conversion to ethanol among the naturally-occurring yeasts [54]. *Sc. stipitis* is widespread in nature, especially in xylose-rich habitats [42]. Its genome serves as the main reservoir of genes for expression in yeast strains incapable of pentose assimilation or fermentation, especially in *S. cerevisiae* [6]. Another common xylose-fermenting yeast is *Sc. schehatae*. It is found in different ecological niches in many geographical zones, including South Africa, Brazil, Poland, and China (Table 1). Despite its established ability to ferment xylose, the industrial use of these yeasts is still problematic due to low ethanol yields from lignocellulosic substrates and the need for strict control of oxygen [55].

As yeast diversity of new habitats and geographical regions is explored, new species are regularly added to the genus of xylose-assimilating yeasts *Scheffersomyces*. Only three *Scheffersomyces* species, *S. segobiensis, S. spartinae,* and *Sc. stipitis*, were known in 2011 when the last edition «The Yeasts: a Taxonimic Study» has been published [42]. Since then more than ten novel *Scheffersomyces* species have been described, most of which possess a xylose-fermenting ability (Table 2). Despite the constant increase in newly-discovered xylose-fermenting yeasts, *Sc. stipitis* remains the most efficient ethanol producer from xylose [6].

Genus *Spathaspora* includes 22 yeast species and some of the most efficient ethanol producers from xylose, including *Sp. passalidarum* [56] and *Sp. arborariae* [57]. *Sp. passalidarum* is an especially promising producer of second-generation bioethanol. It exhibits exceptionally high ethanol yields from xylose that can be compared to those produced by *Sc. stipitis* [58]. Interestingly, *Sp. passalidarum* can convert xylose to ethanol with higher efficiency than from glucose [59].

Table 2. **Novel xylose-fermenting yeasts isolated in the last decade**

Yeast genus	Yeast species	Reference
Scheffersomyces	*Sc. cryptocercus*	Urbina et al, 2013 [19]
	Sc. illinoinensis, Sc. quercinus, Sc. virginianus	Urbina et al., 2012 [47]
	Sc. hehanensis	Ren et al., 2014 [16]
	Sc. titanus	Liu et al., 2016 [37]
	Sc. stambukii	Lopes et al., 2018 [48]
	Sc. jinghongensis, Sc. paraergatensis, Sc. anoplophorae	Jia et al., 2020 [30]
Blastobotrys	*B. bombycis*	Barretto et al., 2018 [34]
Candida	*C. kantuleensis*	Nitiyon et al., 2018 [23]
	C. xylosifermentans	Kaewwichian et al., 2019 [46]
Spathaspora	*Sp. boniae*	Morais et al., 2017 [43]
	Sp. girioi, Sp. hagerdaliae, Sp. gorwiae	Lopes et al., 2016 [26]
	Sp. allomyrinae	Wang et al., 2016 [36]
	Sp. elongata, Sp. mengyangensis, Sp. jiuxiensis, Sp. parajiuxiensis, Sp. rosae	Lv et al., 2020 [49]
Sugiyamaella	*Su. xylanicola*	Morais et al., 2013 [14]
	Su. bahiana, Su. bonitensis, Su. valenteae, Su. xylolytica	Sena et al., 2016 [44]
	Su. yunanensis	Shi et al., 2021 [29]

Several new *Spathaspora* species were recently described, including *Sp. girioi, Sp. hagerdaliae, Sp. gorwiae* [26], and *Sp. boniae* [43]. Though they proved to be less efficient ethanol producers than *Sp. passalidarum*, the final ethanol concentration reached up to 8.8 g/L (or 20—54% efficiency of xylose conversion) [26, 43].

A new genus of xylose-assimilating yeasts *Sugiyamaella* associated with rotting wood and insect frass was established by Kurtzman [60]. In the following years, several xylose-fermenting *Sugiyamaella* species have been discovered, including *Su. bahiana, Su. bonitensis, Su. valenteae,* and *Su. xylolytica* [44], *Su. xylanicola* [14], *Su. yunanensis* [29] (Table 2). The conversion of xylose into ethanol by *Sugiyamaella* yeasts is rather low, the fermentation efficiency being 3.83—37.18% of the theoretical yield [44].

P. tannophilus is a unique representative of xylose-fermenting yeasts as there are only a few known strains of this yeast species, isolated from tanning fluids. This species is the only member of genus *Pachysolen* [61]. It was among the first yeasts discovered to be able to ferment xylose [62]. The following screenings for xylose-fermenting yeasts revealed other more efficient ethanol producers. Recently, these yeasts have been studied as potential xylitol producers from agricultural residues [63].

As the ability to ferment L-arabinose was demonstrated only for few yeast strains, belonging to *Candida* and *Meyerozyma* genera [22, 40], there are not sufficient data to draw any conclusion on the taxonomy of L-arabinose-fermenting yeasts.

The conversion efficiency of xylose to ethanol by many xylose-fermenting yeasts of *Sugiyamaella, Scheffersomyces* and *Spathaspora* clades is too low for cost-effective ethanol production. However, it could be increased by the optimization of fermentation conditions. Also, these yeasts could become a source for new genes to introduce into other host yeasts to improve their productivity.

Biotechnological application of pentose-fermenting yeasts. The main and best-studied field for pentose-fermenting yeasts in biotechnology is their employment in the production of second-generation ethanol. This group of yeasts can serve as the main ethanol producer during the fermentation step and as a source for genes relevant for pentose transport and metabolism [6]. *Sc. stipitis* was considered for a long time as the most promising candidate among naturally occurring yeasts for bioethanol production from lignocellulosic substrates due to its highly efficient xylose conversion into ethanol, producing up to 41 g/L ethanol [53]. *Sc. stipitis* can utilize all the major sugar components of lignocelluloses and has the capacity to

Table 3. **New biotechnological applications of naturally-occurring pentose-fermenting yeasts**

Product	Yeast species	Substrate	Product concentration/yield	Reference
Xylitol	*Sp. passalidarum*	Synthetic medium	10.58 g/L	[69]
	Sp. amazonensis	Sugarcane bagasse and straw	20.11g/L	[70]
	Sp. hagerdaliae	Soybean and oat hulls	0.11—0.33 g/g sugar	[71]
	Su. bahiana, Su. bonitensis, Su. valenteae, Su. xylolytica	Synthetic medium	7.04—10.74 g/L	[44]
	P. tannophilus	Corncob	0.80 g/g sugar	[72]
	P. tannophilus	Corncob, rice straw, and wheat straw	0.81 g/g sugar	[73]
Arabitol	*Sc. shehatae*	Synthetic medium	0.35 g/g L-arabinose	[28]
Single cell protein	*Sp. passalidarum*	Synthetic medium	0.12 g/g	[69]
	Sc. stipitis	Potato waste pulp	7.9—8.6 g/L	[74]

ferment glucose, xylose, mannose, galactose, and cellobiose [53]. However, there are several serious drawbacks for the full-scale utilization of this yeast on the industrial level. First, xylose assimilation and fermentation by *Sc. stipitis* are inhibited by the presence of hexoses, mainly glucose, released during the breakdown of lignocellulose [64]. Second, ethanol yields are greatly affected by the formation of by-products, especially polyols, and the possible concurrent utilization of ethanol by yeasts as a carbon source [59, 65]. Third, *Sc. stipitis* possesses low tolerance to many stress factors that arise during bioethanol production, including ethanol [65] and inhibitory compounds formed as a result of lignocellulose hydrolysis (furans, carboxylic acids, and phenols) [66]. *Sc. stipitis* is probably a main reservoir of the genes to be introduced into *S. cerevisiae* to construct efficient strains for the production of second-generation ethanol [6].

Recently, another yeast species *Sp. passalidarum* has attracted considerable attention due to its ability to rapidly consume xylose and efficiently ferment xylose to ethanol, especially under anaerobic conditions. *Sp. passalidarum* has a considerable advantage over *Sc. Stipites:* it does not require strict oxygen control for xylose fermentation [56]. Interestingly, ethanol production from xylose by *Sp. passalidarum* has been shown to be higher than from glucose, and *Sp. passalidarum* can ferment both sugars simultaneously [59]. The largest drawback for industrial application of *Sp. passalidarum* to the bioethanol production is its high sensitivity to many inhibitory compounds that are formed during lignocellulose hydrolysis [56]. A number of studies focus on the improvement of its tolerance through genetic and evolutionary engineering [67, 68].

Many studies on pentose fermentation using yeasts are directed at the genetic manipulation of the already existing efficient ethanol producers, mainly *S. cerevisiae* [57]. Many studies also focus on the improvement of naturally-occurring pentose-fermenting yeasts [7, 56]. A lot of effort has been spent on the construction of recombinant yeast strains capable of fermenting pentose at levels comparable to glucose and withstanding stress conditions that arise during lignocellulose hydrolysis and fermentation. However, the efficient yeast strain to make ethanol production from lignocellulose viable has not yet been developed [57]. For the cost-effective industrial-scale lignocellulose conversion into ethanol, the discovery or the construction of a robust microbial strain capable of efficient fermentation of both hexoses and pentoses is crucial. The search for new pentose-fermenting strains that could become either potential ethanol producers or sources for new promising genes is still ongoing.

In addition to ethanol production from plant biomass, another promising application for pentose-assimilating and fermenting yeasts is their employment as producers of other chemicals including sugar alcohols, or polyols, such as xylitol, arabitol, and erythritol, as well as various organic acids and single cell protein [4]. Polyols are considered sugar substitutes as they possess high sweetening power and a comparatively low glycemic index. They could be used in various food and pharmaceutical products as sweeteners, stabilizers, and texturizing agents [4]. Most research on polyol production by pentose-fermenting yeasts focuses on xylitol production. The latest research on pentose-fermenting yeasts as promising producers of polyols and other chemical compounds from plant biomass is presented in Table 3.

Conclusions. In summary, the focus of this review is patterns of distribution, biodiversity, and potential applications of pentose-fermenting yeasts. Yeasts are found in a wide variety of habitats in nature, especially those that are rich in sugars. Wood-associated substrates, which often contain pentoses D-xylose and L-arabinose, rarely found in other sources, establish a unique and suitable habitat for many pentose-assimilating and fermenting yeasts. Many novel pentose-fermenting yeast species have been isolated and described since the first report on xylose fer-

mentation by yeasts, and many more sill remain undiscovered. Most such novel species belong to genera *Scheffersomyces, Spathaspora, Sugiyamaella, Candida*. Pentose-fermenting yeasts are promising candidates for the production of second-generation bioethanol. Genomes of these yeasts could provide new insights and targets for genetic manipulation and improvement of other industrial strains, so the search for novel pentose-fermenting yeasts with unique metabolic systems in previously unexplored or poorly explored regions and habitats is ongoing.

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ДРІЖДЖІ, ЩО ЗБРОДЖУЮТЬ ПЕНТОЗИ: ЕКОЛОГІЯ, РІЗНОМАНІТТЯ ТА ВИКОРИСТАННЯ

За останні десятиріччя світова енергетика зазнала величезної трансформації у зв'язку з переходом від традиційних невідновлювальних корисних копалин до все ширшого застосування відновлювальних енергетичних ресурсів — енергії вітру, сонця, води та біопалив. Лігноцелюлозна біомаса є найбільшим відновлювальним джерелом вуглеводів на Землі та може бути одним з найважливіших субстратів для отримання біопалив, зокрема біоетанолу. Широкомасштабне продукування біоетанолу проводять переважно на базі цукровмісних та крохмалевмісних субстратів з використанням дріжджів *Saccharomyces cerevisiae,* які здатні до швидкої та ефективної конвертації гексоз до спирту та мають високу стійкість до стресових факторів. Головний недолік *S. cerevisiae* як потенційного продуценту спирту з лігноцелюлозних субстратів — неможливість асиміляції та ферментації пентозних цукрів, які складають значну частку цукрів деревини. У зв'язку з цим пріоритетним напрямком є пошук та дослідження дріжджів, здатних до ефективного продукування спирту з пентозних цукрів. У цьому огляді представлено дані щодо природних середовищ проживання, географічного поширення, таксономічного положення та потенційного застосування природних дріжджів, що здатні до ферментації пентоз. Дріжджі, що зброджують пентози, переважно виділяють з лігноцелюлозних субстратів та екологічних ніш, пов'язаних з ними. Одним з таких важливих джерел цієї групи дріжджів є гниюча або мертва деревина, яка в результаті гідролітичної дії мікроорганізмів містить пентозні цукри D-ксилозу та L-арабінозу. Такі субстрати є унікальним середовищем для репродукції дріжджів, що ферментують пентози,

оскільки такі цукри рідко зустрічаються у вільному доступі в природі. Кишківник різноманітних комах, що харчуються деревиною, також є важливою екологічною нішею для дріжджів, що зброджують ксилозу. Інші природні джерела, з яких виділяли цю групу дріжджів, включають грунт, рослинні субстрати, кишківник травоїдних. Дріжджі, що ферментують пентози, мають широке географічне поширення та були знайдені майже на кожному континенті. В останні роки виявляють десятки нових видів цієї групи дріжджів в раніше недосліджених або мало досліджених локаціях на кшталт Бразилії, Китаю та деяких азійських країн. Надано дані щодо таксономічного положення дріжджів, що зброджують пентози. Активні продуценти етанолу з ксилози відносять до представників родів *Scheffersomyces, Candida, Spathaspora*, *Sugiyamaella, Pachysolen*, дріжджі з найвищою зброджувальною активністю представлені видами *Sc. stipitis* та *Sp. passalidarum*. Переважна частина досліджень, що стосується біотехнологічного потенціалу дріжджів, здатних до ферментації пентоз, присвячена залученню їх до продукування біоетанолу другого покоління з лігноцелюлози, або як безпосереднього учасника процесу на стадії ферментації, або як джерела генів для інтродукції в інші промислові штами дріжджів. Узагальнено дані щодо останніх досліджень потенційного біотехнологічного застосування цієї групи дріжджів, у тому числі і як продуцентів багатоатомних спиртів. Отже, пошук природних дріжджів, здатних до ферментації пентоз, особливо в екологічних нішах, що пов'язані з лігноцелюлозними субстратами, в раніше недосліджених або малодосліджених географічних локаціях є пріоритетним напрямком, який дозволить не тільки розширити знання про біорізноманіття та генетичні системи цієї групи дріжджів, але й виявити ефективних продуцентів для біотехнологічного застосування.

Ключові слова: *дріжджі, ферментація пентоз, екологія, застосування дріджів.*