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REVIEW

Ecological and Biogeographical Features of *Saccharomyces paradoxus* Batschinskaya Yeast and Related Species: I. The Early Studies

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Abstract—The review deals with the early studies of *Saccharomyces paradoxus* (syn. *S. cerevisiae* var. *tetrasporus*) yeast. The data demonstrate strong evidence that, in contrast to the well-known cultivated *Saccharomyces* yeasts (baker, wine, spirits, and beer yeast), wild *Saccharomyces* yeasts are often found in natural habitats, such as exudate and leaf litter of trees, decaying wood, soil, and insect intestines. These yeasts form a potentially valuable gene pool for research and breeding programs.

Keywords: *Saccharomyces paradoxus,* wild yeast, yeast biogeography, yeast ecology, tree exudates, soil, *Drosophila*

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Genetic and molecular investigation of the *Saccharomyces* yeasts revealed a new gene pool for basic and applied research, namely, the sibling species of *S. cerevisiae* Meyen ex Hansen: *S. arboricola* Wang et Bai, *S. bayanus* Saccardo, *S. cariocanus* G. Naumov et al., *S. kudriavzevii* G. Naumov et al., *S. mikatae* G. Naumov et al., *S. paradoxus* Batschinskaya sensu G. Naumov [1–10]. Wild *S. paradoxus* yeasts, first isolated and studied in Russia [11–16], are taxonomically the closest species to the cultivated yeasts *S. cerevisiae*. In this paper we present original descriptions of the *S. paradoxus* yeasts from different regions of the world. Using molecular genetic methods, the presence of at least four different natural populations of *S. paradoxus* was shown: European [19–21], Far Eastern [19, 21, 22], Hawaiian [21, 23] and North American [21, 24, 25]. The sibling species of *S. cerevisiae* and *S. paradoxus* were also found, namely *S. cariocanus, S. kudriavzevii*, and *S. mikatae* [3]. The synonyms of *S. paradoxus* are *S. mangini* var. *tetrasporus* (Beijerinck) Stelling-Dekker, *S. cerevisiae* var. *tetrasporus* (Beijerinck) Phaff et al., *S. cerevisiae* var. *terrestris* Jensen, and *S. douglasii* (nom. nud.) [16, 26, 27]. The *S. paradoxus* yeasts may be important for applied science [28, 29]; they have been found in the grapes and in the winemaking process [14, 30, 31].

Europe. Batschinskaya [11], on the basis of the studies of two strains isolated in 1913 from the exudate of oak *Quercus pedunculata* Ehr. near the Main Botanical Garden in St. Petersburg and from the elm tree (*Ulmus campestris* Sm.) exudate in the Poltava region, was the first to describe *S. paradoxus* yeast unable to utilize maltose. An isolate of this species from the exudate of ash-tree *Fraxinus excelsior* was also reported by Nadson and Krasil'nikov [12]. There is a reason to presume that the latter strain is deposited in the Dutch collection under accession no. CBS 432. At least, this strain is known to be deposited into CBS by Guillermond, who received it personally while visiting Nadson's laboratory in 1925 [17]. The species name *paradoxus* was associated by Batschinskaya and subsequently by Nadson and Krasil'nikov with its unusual life cycle, namely, its ability to form a complex zygote from all four spores of an ascus. The later studies of Guillermond [17] and Hjort [18], however, did not confirm this "phenomenon". Similar to *S. cerevisiae*, *S. paradoxus* spores within ascus copulate only in pairs and only with those of the opposite mating type.

Hereinafter, the spices are considered to belong to the genus *Saccharomyces* according to the contemporary classification [8]. Batschinskaya had predecessors in the detection of *Saccharomyces* yeast in oak exudates. The first to mention are Lindner and Ludwig, who have isolated the German strains nos. 689–691 and T, V, respectively, for which the physiological characteristics and descriptions are known, as well as the photographs of their mass ascospores and vegetative cells [32, 33]. *S. tetrasporus* CBS 406 yeast, isolated by Beijerinck from the oak-tree exudate in the Netherlands, should also be mentioned; unfortunately, their taxonomic description is absent. The latter species are also known as *S. mangini* var. *tetrasporus* (Beijerinck) Stelling-Dekker [34] and *S. cerevisiae*

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Hansen var. *tetrasporus* (Beijerinck) Phaff et al. [35]. Isolation of *S. globosus* Beij., and *S. minor* Engel from oak tree exudates by Beijerinck was also reported (Oudemans, 1914; cited from Nadson [36]).

The European soil isolates of *Saccharomyces* yeasts should be mentioned. An Italian scientist Capriotti conducted numerous studies of yeast flora of the soils of several European countries (Italy, Spain, Holland, Sweden, and Finland) [37–45]. He isolated wild yeasts *S. cerevisiae* (=*S. ellipsoideus*) Hansen and *S. mangini* Guilliermond from many regions, even in the countries not practicing winemaking. The taxa were differentiated on the bases of their ability to ferment maltose, Mal^+ and Mal^-, respectively. According to Jensen [46], yeasts are important for soil metabolism. He studied the Danish forest soils and isolated up to 500000 yeast cells per gram of dry soil. On the basis of investigation of eight soil isolates, he described a new taxon *S. cerevisiae* var. *terrestris*, which was characterized by very slow fermentation of maltose and melezitose. Two isolates were classified as a new yeast *S. cerevisiae* var. *fructuum*, which does not ferment maltose. Lund [47] found *S. cerevisiae* var. *ellipsoideus* in the soils of a Danish beech forest and coastal areas. Peat bog soils are another ecological niche of *Saccharomyces*. The *Saccharomyces* yeasts were found in both lowland and upland peat-bog soils of Belorussia [48, 49], comprising 18.3% of the total yeast population. Golubev and co-authors [50] found 20% of *Saccharomyces* yeasts in one of the samples of lowland bog peat from the Kashira region near Moscow. The yeasts, in our opinion tentatively *S. cerevisiae/vini*, were isolated from the rhizosphere and phyllosphere of forest trees near Kiev [51–53].

Asia. Saito and Ootani were probably the first to isolate the *S. paradoxus* from the exudate of an *Q. acutissima* oak-tree in Japan [54]. Kudryavtsev discovered *S. paradoxus* in oak-tree exudates in the Far East of Russia in 1934 [14, 30, 55, 56]. Later, Japanese researchers reported the isolation of *Saccharomyces* yeasts from exudates of various trees, particularly oaks, as well as from soil [57–62]. Most often, these yeasts were isolated under the name of *S. cerevisiae* var. *tetrasporus*. Yoneyama [58] was the first to report close relation between *S. paradoxus* and *S. cerevisiae* var. *tetrasporus*. The table shows the distribution and species names of *Saccharomyces* yeasts isolated from the exudates of various trees in Japan according to Kodama [60]. Banno and Mikata [62] reported the isolation of various *Saccharomyces* yeasts from environmental sources (soil, litter of leaves, flowers, bark, and mushrooms). Most of *Saccharomyces* isolates originated from soils and leaf litter. The *Saccharomyces* yeasts isolated in Japan may be divided into three groups: (1) not fermenting and/or poorly fermenting maltose, namely *S. cerevisiae* var. *tetrasporus* and *S. chevalieri*; (2) fermenting melibiose, namely *S. uvarum*; and (3) not fermenting galactose, namely *S. bayanus*.

North America. According to Dobzhansky, various yeasts are natural food for *Drosophila* and may affect selection of different populations of these flies [63]. Several investigations of the yeasts from *Drosophila* intestine and their habitats were conducted and it was shown that live *S. cerevisiae* could predominate in *Drosophila* intestine [63, 64]. Phaff and co-authors [35, 65] found relatively high abundance of *S. cerevisiae* var. *tetrasporus* and *S. uvarum* in the intestines of several *Drosophila* species. They also investigated many exudates of different trees, and *S. cerevisiae* var. *tetrasporus* and *S. uvarum* were occasionally found only in the exudate of elm-tree *Ulmus carpinifolia* [66, 67]. Despite extensive research, *S. cerevisiae/S. cerevisiae* var. *tetrasporus* have not been found in the exudate of oak trees of North America, for a long time [67–70]. However, research in Southern Arizona revealed *S. cerevisiae* in the exudate of *Q. emoryi* oak and *Populus fremontii* poplar growing near water sources, as well as in *Drosophila carbonaria* associated with these trees [71]. Association of *S. cerevisiae* and *S. uvarum* with fungal galls (black knot disease) of *Prunus* and *Malus* trees from Canada deserves mentioning [72]. These species were also isolated from *Drosophila* of a conifer-oak forest park in Ontario, Canada [73].

The studies of soil yeast flora of North America are also worth mentioning. Zambrano and Casas-Campillo [74] isolated 200 yeast strains from 17 samples of tropical and subtropical soils of Mexico. The yeast cell count was 1000 to 100000 per gram of dry soil, with the *Saccharomyces* yeasts comprising up to 75%. Capriotti [42] compared occurrence of yeasts in some soils of North America and Europe using his standard enrichment technique. He analyzed 145 yeast isolates from 10 soil samples from the Key Biscayne Island, Florida, which separates the Biscayne Bay from the Atlantic Ocean; the mangrove vegetation occupies the western side of the island, and the eastern side is a sandy beach. The *Saccharomyces* (*S. ellipsoideus*) yeasts were found in a single sample, where they comprised 10% of the total yeast population. According to another Capriotti publication [45], 38 other soil samples were also studied, including 2 samples from Key Biscayne Island, 36 from the North-East, Pennsylvania, Key Largo Island, and Florida, as well as 12 from Alaska. *Saccharomyces* were found in four samples: *S. ellipsoideus* (11.7%) in non-cultivated soil of Alaska and in garden soil of Pennsylvania and *S. carlsbergensis/S. uvarum* (11.6%) in the vineyard of Pennsylvania and New Jersey meadows.

South Africa, South America and Hawaii. The yeast flora of these regions, particularly the distribution of *Saccharomyces*, is insufficiently studied. Six *Saccharomyces* isolates from the soils of South Africa were described: 4 strains of *S. cerevisiae*, including strain CBS 2908, one strain of *S. coreanus* (CBS 2888) and one strain of *S. uvarum* [75, 76]. The *Saccharomyces* yeasts were isolated from *Drosophila* and, in minor quantities, from the natural product of fungal fermen-

The *Saccharomyces* yeasts isolated by Kodama [60] from trees exudates and the sites of their isolation

Tree	Geographical region	Tree	Geographical region
S. cerevisiae Meyen ex Hansen			
Acer mono	Hokkaido	*Rhus* sp.	Gunma
Tilia japonica	"	*Lagerstroemia indica*	Saitama
Quercus sp.	"	*Camellia japonica*	Kanagawa
Tilia japonica	"	*Celtis sinensis* var. *japonica*	"
Ulmus sp.	"	*Quercus acutissima*	"
Quercus sp.	Aomori	*Quercus* sp.	"
Aesculus turbinala	"	*Quercus acutissima*	Tokyo
Vitis coignetiae	"	*Q. dentata*	"
Quercus sp.	"	*Betula ermani*	Nagano
Fagus crenata	"	*Acer* sp.	"
F. crenata	"	*Acanthopanax sciadophylloides*	"
Celastrus orbiculatus	Akita	*Betula* sp.	"
Alnus japonica	"	*Quercus* sp.	"
Quercus acutissma	"	*Betula maximowiczii*	"
Cornus controversa	"	*Quercus myrsinaefolia*	Ishikawa
Quercus sp.	"	*Carpinus* sp.	"
Aralia elata	"	*Fagus japonica*	Gifu
Acer sp.	"	*Prunus* sp.	Shizuoka
Quercus sp.	"	*Quercus* sp.	"
Morus sp.	Iwate	*Quercus serrata*	"
Platycarya rhoifolia	"	*Castana crenata*	"
Quercus mongolica	"	*Betula grossa*	Miye
Acer mono	"	*Betula* sp.	"
Quercus sp.	"	*Magnolia* sp.	"
Quercus myrinaefolia	"	*Stewartia monadelpha*	"
Betula ermnai	"	*Acer* sp.	Nara
Acer mono	"	*Acer mono*	"
Alnus japonica	"	*Quercus acutissima*	"
Betula ermnai	"	*Betula grossa*	"
Magnolia obovata	Yamagata	*Paulownia* sp.	"
Quercus sp.	"	*Quercus myrsinaefolia*	Nara
Camellia japonica	"	*Q. glauca*	Hyogo
Prunus grayana	"	*Q. dentata*	Hiroshima
Aralia elata	"	*Q. variabilis*	"
Acer mono	"	*Q. mongolica*	"
Prunus sp.	"	*Quercus* sp.	"
Sorbus alnifolia	"	*Quercus mongolica*	"
Micromeles alnifolia	"	*Quercus* sp.	Yamaguchi
Quercus mongolica	"	*Morus alba*	"
Q. myrsinaefolia	Fukushima	*Camellia japonica*	"
Platycarya strobilicae	"	*Quercus* sp.	Kochi
Acer pyenanthunm	"	*Ilex integra*	Kumamoto
Prunus sp.	"	*Quercus dentata*	Saga

Table. (Contd.)

Tree	Geographical region	Tree	Geographical region
Castanea crenata	"	*Rhus* sp.	"
Stewartia monadelpha	"	*Quercus dentata*	Kagoshima
Acer matumurae	"	*Rhus* sp.	"
Symptocos myrtacea	"	*Camellia japonica*	"
Magnolia sp.	"	*Camellia* sp.	"
Quercus acutissima	Miyagi	*Cornus controversa*	Miyazaki
Quercus sp.	Gunma		
	S. uvarum Beijerinck		
Platycorya rhoifolia	Hokkaido	*Aralia elata*	Kanagawa
Quercus sp.	Aomori	*Juglans* sp.	Nagano
Aesculus turbinala	"	*Betula* sp.	Nara
Acer mono	"	*Fagus crenata*	Tottori
Alnus japonica	Akita	*Quercus mongolica*	"
Quercus acutissima	"	*Camellia sasangua*	Yamaguchi
Quercus mongolica	"	*Quercus dentata*	Kochi
Cornus controversa	"	*Lagerstroemia* sp.	Saga
Quercus mongolica	Yamagata	*Quercus dentata*	Kagoshima
	S. chevalieri Guilliermond		
Vitis vinifera	Akita	*Acer* sp.	Hyogo
Betula sp.	Nagano	*Quercus acutissima*	Kagoshima

tation of wood residues (huempe) from the rain forests of Brazil and the southern part of Chile [77, 78]. The strains of *S. uvarum* (UWO (PS) 99-808.3 and UWO (PS) 99-807.1.1) were isolated from the exudate of the beech tree *Nothofagus* sp. from Patagonia, Argentina, (UWO (PS)—University of Western Ontario, Department of Plant Sciences, Culture Collection, Canada). The *S. cerevisiae/S. oviformis* yeasts not fermenting galactose were isolated from the exudate of sandalwood *Myoporum sandwicense* in Hawaii [79].

Utilization of maltose is an important characteristic of cultivated *Saccharomyces* yeasts. As was mentioned above, a number of authors noted weak maltose fermentation or inability to ferment this sugar by environmental *Saccharomyces* isolates. Such strains were usually able to assimilate maltose aerobically. Kudryavtsev [13] and Yoneyama [59] suggested that the transformation of wild *Saccharomyces* yeasts into cultivated ones resulted from the evolutionary development of the "maltose fermentation" feature. According to earlier reports [13–15], *S. paradoxus* can adapt to maltose fermentation, probably as a result of both regulatory and mutational variability. Genetic determination of aerobic assimilation of maltose in the *Saccharomyces* strains unable to ferment it remains unclear. The α-glycosidase (maltase), which hydrolyses maltose to glucose, is an intracellular enzyme [80]. Thus, maltose fermentation obviously requires not only the active α-glycosidase, but also active maltose transport into the cell. The only known report [81] on genetics of maltose assimilation by *S. cerevisiae* gave evidence that the analysis of a hybrid of the strains differing in these characteristics showed that while assimilation of maltose was controlled by a single gene, probably the α-glycosidase gene (*MAL*), the rate of this process was controlled by two polymeric noncumulative and non-complementary genes V1 and V2. The role of these three genes remains unknown. The authors [81] also found that the shift in maltose concentration from 2 to 4% resulted in delayed (up to 12 days) fermentation of this sugar by the segregants with fast and slow maltose assimilation. Assimilation of maltose in this case was probably due to the low maltose transport activity. Two possibilities to enhance the low capability of some yeast to metabolize sugars

should be considered: increasing sugar concentration from 0.5 to 2–10%, and is the addition of yeast extract into the medium [82, 83].

CONCLUSIONS

The general opinion, especially among geneticists and applied microbiologists, that *Saccharomyces* yeasts are of exclusively cultivated origin (baking, wine, spirits, and beer yeast) is not correct. The natural populations of yeast of the genus *Saccharomyces*, primarily *S. paradoxus*, which differ in their ability to ferment sugars (maltose, melibiose, and galactose) inhabit trees exudates, insect intestines, leaf litter, and soil.

Correct species assignment of natural *Saccharomyces* strains by modern techniques and determination of their relationship to the cultivated *S. cerevisiae* yeasts was a task for geneticists and molecular taxonomists. Studies of the evolutionary genetics of maltose utilization by wild and cultivated strains were also needed. These issues will be discussed in our next article.

Finally, I would like to mention the outstanding role of the zymologists V.I. Kudryavtsev [14] and H.J. Phaff [84] in studying ecology and biogeography of yeast, particularly *S. paradoxus*/*S. cerevisiae* var. *tetrasporus*.

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