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BREVIBACILLUS REUSZERI AS A POTENTIAL RESOURCE FOR SUSTAINABLE AGRICULTURE

The species Brevibacillus reuszeri was separated into a specific taxonomic unit 30 years ago, during which it has been studied. The aim of the study was to collect and analyze the available scientific information on the species Brevibacillus reuszeri. A search was conducted in scientific literature databases using the queries "Brevibacillus reuszeri" and "B. reuszeri". Only studies that identified B. reuszeri using MALDI-TOF, phylogenetic or phylogenomic methods were included in the review. Brevibacillus reuszeri is characterized by the ability to produce chitinases with antifungal activity, bacteriocin and the ability to counteract environmental pollution by heavy metals and the ability to hydrolyze polyurethane. Paradoxically, this species is also a plant growth-promoting rhizobacterium with an unusual activity, the ability to promote mycorrhiza formation. Further research should test the possibility of developing biological products based on cultures of this species for bioremediation and plant growth promotion. Another promising area is the search for new antimicrobial compounds based on products of unidentified biosynthetic clusters of Brevibacillus reuszeri strains.

Key words: Brevibacillus, Plant-growth-promoting rhizobacteria, Mycorrhiza-helping bacteria, angifungal activity, bacteriocin.

Introduction

The species of the genus *Brevibacillus* are studied extremely unevenly [22]. The aim of the study was to collect and analyze the available scientific information on the species *Brevibacillus reuszeri*. As the topic for this review was chosen *Brevibacillus reuszeri* because of the presence of determinants of antimicrobial ribosomal peptide biosynthesis in its published genome, which coincides with the current scientific interests of the authors of this work. As of 2025, enough data have been collected to talk about the ecophysiological individuality of this species.

The species *Bacillus reuszeri* was described in 1995 as a result of a polyphasic taxonomic analysis of a series of strains previously classified as *B. brevis* [29]. It was named in honor of the American microbiologist Herbert W. Reuszer from Purdue University, who isolated the strain that became the type of this species. Unfortunately, there is little biographical information on this specialist, except for his special works.

Over the next 25 years, with the development of molecular genetic methods of systematics, species of the genus *Bacillus* were divided into dozens of new genera.

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Brevibacillus was one of the first to be isolated [30] as a result of comparison of 16S rRNA nucleotide sequences of the bacterial group in the *Bacillus brevis* cluster. Additionally, the similarity of the *Bacillus brevis* group was proven by the detection of serologically related S-layer proteins. In addition, segments of the 16S rRNA nucleotide sequence were found to be group-specific for all members of the genus *Brevibacillus*. *Bacillus reuszeri* was reclassified as *Brevibacillus reuszeri* comb. nov. Together with it, the genus *Brevibacillus* includes *B. reuszeri* and nine other species from the former intrageneric cluster *Bacillus brevis*. Today, the species *Brevibacillus reuszeri* belongs to the domain Bacteria, type Bacillota, class Bacilli, order Caryophanales, family *Paenibacillaceae*, genus *Brevibacillus* (date of access to the List of Prokaryotic names with Standing in Nomenclature – 14.04.2025 [24]).

The type strain of *B. reuszeri* was isolated from soil and is designated NRRL NRS-1206 (alternative numbers: DSM 9887, ATCC 51665, CIP 104543, IFO 15719, JCM 9170, NBRC 15719, BCRC 17828, CGMCC 1.3106, LMG 16012, NCIMB 13367). The strain is deposited at the Japan Collection of Microorganisms, Saitama, Japan, as JCM 9170 and at the Institute of Fermentation, Osaka, Japan, as IFO 15719 [29].

The scientific literature databases were searched using the queries "Brevibacillus reuszeri" and "B. reuszeri". Only papers where *B. reuszeri* was identified using MALDI-TOF, phylogenetic or phylogenomic methods were used for the review.

1. Features of morphology, physiological and biochemical characteristics

The fundamental traits of this species has not been adjusted over the past 25 years and is based on the original publication [29].

The cells are Gram-positive motile rods with peritrichial flagella, 0.5–0.9 by 2.0–5.0 µm in size. Ellipsoidal spores are formed in swollen sporangia. Colonies are flat, smooth, round and with a smooth edge. No soluble pigment is formed on nutrient agar. Specific S-layer proteins are present. The main fatty acid is anteiso-C15:0 acid. The main quinone is menaquinone 7.

The optimum growth temperature is 30 °C, the maximum is 45 °C, the minimum is 10 °C (the minimum test temperature), and growth is inhibited at 50 °C. Growth of *B. reuszeri* is observed at pH 5.5 and 5.6, at 2% NaCl, but is inhibited at 3% NaCl. It is also inhibited by lysozyme at a concentration of 0.001%.

B. reuszeri is strictly aerobic, catalase-positive and oxidase-negative. Acetylmethylcarbinol is not produced (as determined by the Voges-Proskauer test). The pH of the broth is above 7.0. Hydrogen sulfide, indole and lecithinase (based on the results of the egg yolk test) are not produced. Nitrate is not reduced to nitrite. Casein, gelatin, starch, DNA and urea are not hydrolyzed. Tyrosine is degraded. Citrate, propionate, acetate, fumarate, L-malate, DL-lactate, succinate, L-glutamate, L-aspartate, alginate, gluconate, α-ketoglutarate, malonate and tartrate are not used as carbon sources.

B. reuszeri forms an acid, but not a gas, from D-glucose, D-fructose, maltose, glycerol, D-mannitol, D-cellobiose, D-ribose, and raffinose. However, L-arabinose, D-galactose, lactose, sucrose, D-xylose, trehalose, salicin, D-sorbitol, L-sorbose, D-mannose, melibiose, L-rhamnose, inositol, erythritol, and adonitol are not converted [29].

The genome of *B. reuszeri* was characterized by the presence of different types of carbohydrate-active enzyme families. 85 genes of such enzymes were identified, which is 1.35% of the total number of coding sequences. In particular, it was found that the number of chitinases in *Brevibacillus* was significantly higher than the number of cellulases and hemicellulases. Only in *Brevibacillus panacihumi* JCM 15085 and *B. reuszeri* J31TS6 was observed the only representative of the cellulase family GH9 (endo-glucanase) [12].

2. Genomic characterization

As of 11.04.2025, 7 partial genomic sequences of this species are available in the online GenBank database; the last published one dates back to October 2024.

The G+C content ranges from 46.4 to 47%; the G+C pair content in the genome of the typical NRRL strain NRS-1206^T *in vitro* was estimated at 46.5% [29], and according to the results of *in silico* calculation in [31], it was 46.95%.

The genome sizes of J31TS6 and NRRL NRS-1206T strains are 6.559 mb and 6.98 mb, respectively. Among all *Brevibacillus* species described for 2025, this size is the largest. Until a complete genome assembly is obtained for at least one of the strains of this genus, these estimates should be taken with caution. The genome of the J31TS6 strain is slightly smaller than that of the type species *Brevibacillus brevis* (6.72 mb), but it is the leader in the total number of genes (6580) and coding sequences (6303). A total of 6817 genes were identified in the genome of the NRRL strain NRS-1206^T, including 6463 coding sequences, 254 pseudogenes, 96 tRNAs, and 3 rRNA genes. For the *B. reuszeri* NIT02 strain, 6774 open reading frames, 121 tRNAs, and 10 non-coding RNAs of the Bacillaceae-1 type were found [12, 25, 31].

3. Auto- and synecology of the species *Brevibacillus reuszeri*

Interactions between *B. reuszeri* and other species can be either mutualistic or antagonistic. The former is manifested in the form of promoting plant growth through its role in the development of mycorrhiza and inhibiting the growth of phytopathogenic fungi; the latter partially derives from the former and consists in the ability to inhibit the growth of mycelial fungi and bacteria through the release of various toxic products. Also, strains of this species show the ability to combat the effects of anthropogenic impact on the environment – the presence of heavy metal ions in high concentrations and the decomposition of artificial polymers.

The *B. reuszeri* strain J31TS6 contains about 200 heavy metal resistance genes and ranks second (after *Brevibacillus choshinensis*) among all *Brevibacillus* species in this regard [12]. Interestingly, the studied strains of *B. reuszeri* were also the most active degraders of polyurethanes [12]. The ability of strains of this species to selectively remove As^{2+} from the environment has been shown [6].

Some types of aerobic bacteria form mutualistic symbioses with higher plants. Such microorganisms are called Plant Growth Promoting Rhizobacteria (PGPR). A specific category of such bacteria is Mycorhiza Helping Bacteria (MHB); few of them are known among bacilli, but *B. reuszeri* belongs to this small category. The positive effect of MHBs on plants is exclusively or partially mediated by their ability to promote mycorrhiza development [7].

The strain *Brevibacillus reuszeri* MPt17 was isolated from the mycorrhizosphere of the symbiotic pair *Pinus massoniana* (Lamb.) – *Pisolithus* *tinctorius*. The basidiomycete fungus *Pisolithus tinctorius* is a low-specialized mycorrhizal mycorrhizal organism that forms ectomycorrhiza with both representatives of the gymnosperms (*Abies*, *Pinus*, *Tsuga, Pseudotsuga*) and the angiosperms (*Alnus*, *Betula*, *Eucalyptus*, etc.), and has been used in forestry for many years to promote the survival of seedlings [5]. In experiments [35], the growth of the fungus was significantly stimulated by sterile *B. reuszeri* culture fluid: the dry weight of the mycelium increased by 16.8%.

Acidic polypeptides of the fungal cell wall surface involved in the interaction with the plant rhizoplane may be part of the intercellular adhesion system necessary for hyphal aggregation in ectomycorrhizal plants [16]. Three genes encoding acidic polypeptides PtBrS008, PtBrS054, and PtBrS105, which are hypothesized to be involved in symbiosis regulation, were identified in *P. tinctorius*. The expression of all three acidic polypeptides was increased when *P. tinctorius* interacted with *B. reuszeri* culture fluid. The expression of the *PtBrS054* gene was increased the most among the others – by 4.1 times [35]. The search for an intermediary molecule produced by *B. reuszeri* that increases the expression of *PtBrS* genes seems promising for studying symbiosis processes, since the molecular mechanism of interaction has not yet been described.

Fusarium oxysporum and *Rhizoctonia solani* are two types of phytopathogens that often attack horticultural crops [17]. The main component of fungal cell walls is chitin, so one of the biological control strategies is the use of bacteria that produce chitinolytic enzymes [1]. This method of pathogen control has significant advantages over chemical control, as it does not threaten the rapid emergence of resistant pathogens and does not have a long-term negative impact on the environment.

B. reuszeri was able to completely stop the growth of *R. solani* and partially stop the growth of *F. oxysporum* [18]. The mechanism of protection of the latter is probably due to the presence of glycoprotein compounds in the outer layer of the cell wall, which make up 50–60% of the total cell wall mass [26]. Unfortunately, not all studies on the antagonistic activity of *B. reuszeri* indicate the origin of the strains. It is all the more valuable that in some studies antifungal activity is observed in rhizosphere isolates [20].

There are several approaches to controlling mycotoxin contamination, including physical removal of toxins using binders, enzymatic degradation, or preventive control of toxin contamination using antifungal microbes. Since decontamination of mycotoxins is difficult due to their chemical stability, an easier and more effective approach to controlling mycotoxins is to prevent contamination rather than remove them after they occur [27].

It is known that *B. reuszeri* produces chitinases [12], and therefore it can be used as a biological control agent to prevent fungal infection of plant crops. Indeed, culture filtrates of *B. reuszeri* completely inhibited the germination of conidia from 8 *Fusarium* isolates on ears of maize. These conidia remained intact without germination for at least 21 days of incubation, while the other conidial isolates germinated on the first day. Bacterial isolates of *B. reuszeri* were antagonistic to 48 of the 68 fungal species tested: most *Fusarium* spp. (39 of 46 species), two *Epicoccum* spp. (2 of 2), and one *Alternaria* sp. (1 of 1) were inhibited by the bacterial isolates. However, only a fraction of *Aspergillus* and *Penicillium* species were affected (3 out of 11 and 3 out of 8, respectively). This broad spectrum of action included most of the mycotoxic *Fusarium* spp. and therefore *B. reuszeri* may be a worthy candidate for the development of biological plant protection products [11].

The inhibition of fungal growth from an agar block placed on nutrient medium without contact with a colony of *B. reuszeri* isolate indicates that the substance(s) released from the antagonist are responsible for the inhibition. The nature of the antagonistic activity of the culture filtrate has not been studied, but it is known that this substance is stable and active in solution for 21 days and can be produced by bacteria within 3 days of cultivation [11]. This stability and activity is a significant advantage for a biological control agent, but the degree of safety of this substance has not yet been determined.

According to Gholizadeh et al. [10], bioactive compounds of *B. reuszeri* strain isolated from soil in southern Iran showed antimicrobial properties against *Escherichia coli* and *Staphylococcus aureus, Salmonella typhi* and *Bacillus cereus*; whereas, *Aspergillus niger*, *Candida albicans* and *Pseudomonas aeruginosa* were resistant to their action.

It is known that bacteriocins are produced in the exponential phase, while antibiotics are produced in the stationary phase of growth [21]. Bacteriocins are known for representatives of the genus *Brevibacillus*, in particular, quite non-standard ones, such as encapsulin derivatives [3]. In the stationary phase, the activity of bacteriocins decreases, which may be due to their destruction by proteases [23]. According to Gholizadeh et al. [10], the production of antimicrobial compounds in *B. reuszeri* culture began at the 5th hour of cultivation and reached a maximum level at the 25th hour of bacterial growth, i.e. in the exponential growth phase. After 25 hours of growth, the antibacterial activity of the compounds decreased moderately. The molecular weight of the antibacterial compound is about 40 kDa. Proteinase K inhibits the antimicrobial activity of the identified compounds, which is an additional argument in favor of their peptide nature.

B. reuszeri was detected as part of microbial associations in clinical material [9].

4. Practically useful properties and applications

The properties of some isolates of *B. reuszeri* mentioned in the previous section indicate the prospects of this species as a plant protection agent and potential growth stimulator. Indeed, numerous studies on the effects of *B. reuszeri* inoculation of agricultural plants have reported an increase in yield and nutritional value, as well as an improvement in the general condition of plants. *B. reuszeri* was found to be capable of producing a biotechnologically promising broad-spectrum carbamoylase enzyme and a thermolysin metalloproteinase inhibitor.

Many agricultural soils around the world are deficient in one or more elements necessary to support healthy plants. The use of chemical fertilizers has a negative impact on the complex system of biogeochemical cycles, so there is a growing interest in environmentally sustainable and organic farming methods [8]. One of the possible ways to reduce the negative impact on the environment is to inoculate the soil with PGPR. Given the high costs of producing nitrogen and phosphorus fertilizers, *B. reuszeri* can be a promising alternative as a biofertilizer, as the results of a study by Young et al. 34 showed that at least 50% of chemical fertilizers can be saved if PGPR is applied together with fertilizers or manure.

The success in increasing yields with PGPR was experimentally confirmed when using *B. reuszeri* as a fertilizer supplement in the cultivation of pecan *Carya illinoinensis* (Wangenh.) K. Koch, broccoli *Brassica oleracea* var. *italica* and strawberry *Fragaria* × *ananassa* Duch.

B. reuszeri increases the surface area of the pecan root and causes positive changes in the overall architecture of the root, promoting the growth of mycorrhizal fungi in the soil and the ability to absorb water. After 60 days of cultivation, the content of total phosphorus in the roots and the content of total potassium in the pecan stems were significantly increased by 78% and 111.53%, respectively [28].

In the study of the effect of *B. reuszeri* inoculation on broccoli, it was possible to achieve an increase in broccoli yield by 12%, and the number of heads by 27%; the head diameter and stem diameter also increased. Chlorophyll levels in the leaves increased by 14% [32]. In a study the following year, yields increased by 20% and plant weight increased by 17% [33]. There is also a paper describing the stimulation of eggplant growth and yield by a culture of this species [2].

In addition to simple quantitative indicators of the crop, there are other parameters that can be favorably affected by processing. An important problem of nutrition in developing countries is the lack of micronutrients in food, which is also called hidden hunger. According to studies [32, 33], when cultivated with *B. reuszeri*, the maximum content of such elements as Sulfur (78.5%), Copper (134%), Ferrum (75%), Manganese (98%) and Zinc (80%) increased in broccoli leaves.

Inoculation of the strawberry rhizosphere with *B. reuszeri* bacteria increased the yield by 18.0% [13].

An important method for the synthesis of optically pure L-amino acids is a two-step process involving the enzymatic conversion of substituted L-hydantoins to L-carbamoyl amino acids, followed by the cleavage of the urea residue by L-N-carbamoylase. Because of this, there is a need for a versatile and stable L-N-carbamoylase for the production of L-α-amino acids, which are used in various industrial applications and human health products. A physicochemically stable trimeric native L-N-carbamoylase obtained from the culture of *B. reuszeri* strain HSN1 was characterized, which is characterized by a broader substrate specificity and significantly higher specific activity compared to those reported for L-N-carbamoylases previously [19].

The strain *B. reuszeri* IFO 15719T was found to be capable of producing a thermolysin metalloproteinase inhibitor. The inhibitor is a monomeric protein with a molecular weight of approximately 60 kDa. Compared to the inhibitors of other bacteria investigated in the cited study, the molecular weight of the inhibitor from *B. reuszeri* strain IFO 15719T is much higher and the thermal stability is lower [14].

5. Future prospects

It is worth noting that in the pool of the literature, where *Brevibacillus reuszeri* is mentioned, the identification of its strains is based on the homology of the 16S rRNA gene. Today, the gold standard for identifying microorganisms is phylogenomics, in particular, genome comparison using algorithms that result in an equivalent DNA-DNA hybridization *in vitro*. It can be assumed that at the moment, the name *Brevibacillus reuszeri* refers to a cluster of closely related species in the literature, which, however, does not deprive the analysis of the biology of this group of scientific content.

The antiSMASH database, which stores taxonomically organized information on sets of biosynthetic clusters found in the genomes of archaea, bacteria, and fungi, contains data on the cluster of two strains of *Brevibacillus reuszeri*: *Brevibacillus reuszeri* DSM 9887 and *Brevibacillus reuszeri* J31TS6. The discrepancy between the number of genomic sequences in GenBank and antiSMASH databases is explained by the fact that the genomes in the latter database were filtered on the basis of similarity (to avoid duplication of information) and the degree of fragmentation (to avoid fragmentation of the detected biosynthetic clusters, which would make their analysis impossible) [4]. In the genomes of both strains of this species, 8 biosynthetic clusters were detected, of which one belongs to linear azole-containing peptides and an unidentified ribosomal peptide. Unlike the others, these clusters have no homologues in the MIBiG and antiSMASH databases and are responsible for the synthesis of new biologically active peptides, the isolation, purification and characterization of which remain to be conducted.

Conclusion

B. reuszeri is a widespread, poorly understood species of aerobic spore-forming bacteria. It lives in the soil in association with plants and fungi, improves plant growth, in particular, by promoting the formation of mycorrhiza; it is resistant to heavy metals, can reduce their concentration in the local environment, can grow in areas of industrial emissions, and thus may be involved in bioremediation. It is also capable of synthesizing potentially useful compounds, including polyurethane degradation enzymes, L-N-carbamoylase, chitinase, metalloproteinase inhibitor, and bacteriocin. The unidentified biosynthetic clusters of ribosomal peptides found in the genomes of these strains are subject to further study for the purpose of isolation, purification and analysis of the properties of the compounds whose synthesis they determine.

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BREVIBACILLUS REUSZERI ЯК ПОТЕНЦІЙНИЙ РЕСУРС ДЛЯ ЕКОЛОГІЧНОГО СІЛЬСЬКОГО ГОСПОДАРСТВА

Резюме

Вид Brevibacillus reuszeri було відокремлено в окрему таксономічну одиницю 30 років тому, протягом яких він досліджувався. ***Метою*** *роботи було зібрати та проаналізувати наявну наукову інформацію щодо виду Brevibacillus reuszeri. Було здійснено пошук в базах даних наукової літератури по запи-*

там «Brevibacillus reuszeri» та «B. reuszeri». Для огляду було використано лише роботи, де ідентифікація B. reuszeri виконувалася з використанням MALDI-TOF, філогенетичних або філогеномних методів. Brevibacillus reuszeri характеризується здатністю до продукції хітиназ з антифунгальною активністю, бактеріоцину та здатністю до протидії забруднення середовища важкими металами, та здатністю гідролізувати поліуретан. Парадоксально, що даний вид також є різобактерією, що сприяє росту рослин з незвичайним видом активності – здатністю до сприяння утворення мікоризи. Подальші дослідження мають перевірити можливість розробки біопрепаратів на основі культур штамів даного виду для біоремедіації та сприяння росту рослин. Також перспективним напрямком є пошук нових антимікробних сполук на основі продуктів неідентифікованих біосинтетичних кластерів штамів Brevibacillus reuszeri.

Ключові слова: Brevibacillus, Plant-growth promoting rhizobacteria, Mycorrhiza-helping bacteria, ангифунгальна активність, бактеріоцин.

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