

Rhodococci

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Rhodococci are relatively new objects of environmental and industrial biotechnologies. Their metabolic potential for biodegradation and inactivation of complex pollutants, in addition to their mechanisms of stress resistance, are far from being exhausted. However, one should be conscious that some members of this genus are pathogens, and their number is gradually expanding, which clearly limits the practical application of rhodococci.

actinobacteria

pathogenicity factors

adhesion

autoaggregation

colonization

defense against phagocytosis

adaptive strategies

1. Introduction

Among the stress-tolerant species, actinobacteria of the genus *Rhodococcus* (phylum *Actinobacteria*, class *Actinomycetia*, order *Corynebacteriales*, family *Nocardiaceae*) (available online at: <https://psn.dsmz.de/class/actinomycetia> (accessed on 20 July 2021)) stand out due to their greatest variety of degraded xenobiotics and their complete mineralization of chemical pollutants to simple substances using alternative carbon sources (cometabolism), often followed by useful product formation [1][2][3].

A wide range of actinomycetologists focus on the study of polyextremotolerant rhodococci predominant in anthropogenically disturbed biotopes primarily due to their feasible applications in ecobiotechnologies. Although the study of *Rhodococcus* was, until recently, largely academic, it has now become more applied. This is obviously because, due to their metabolic flexibility, rhodococci do have not many “competitors” in terms of decomposing organic xenobiotics to inorganic products or low-molecular-weight organic fragments that can participate in the natural carbon cycle.

Considerable material is available on the degradation of priority pollutants by rhodococci to aid the understanding of their metabolic pathways. The number of publications is growing on new chemical agents degradable by rhodococci; and *Rhodococcus* genome projects have been launched [4][5][6]. The ability of rhodococci to decompose recalcitrant xenobiotics and resist their toxic effects, in addition to *Rhodococcus* survival strategies under the combined actions of ecotoxicants and other exogenous harmful factors, are well documented [5][7][8][9][10][11][12][13][14][15][16][17][18][19][20].

The immanent property of rhodococci is to synthesize cell components due to gaseous (C_3 – C_4) and liquid *n*-alkanes. Because of the capability of *Rhodococcus* to engage in oxidative transformation and degradation of natural and anthropogenic hydrocarbons, they are the least dependent on the external environment, avoid

substrate competition, and survive in hydrocarbon-polluted environments. Thus, rhodococci are key players in maintaining the environment's sustainability, active participants in the biogeochemical cycles of the biosphere, and significant contributors to the natural restoration of oil-polluted ecosystems and a carbon-free atmosphere of the Earth. This is their most general planetary function [21][22][23][24].

Our long-term geographically-tailored study of *Rhodococcus* diversity in anthropogenically loaded soils and aquatic ecosystems resulted in the gathering of factual material, namely, identification of numerous pure non-pathogenic cultures and descriptions of their characteristics. It was experimentally confirmed that the characteristic of a constant number of *Rhodococcus* not influenced by sharp seasonal fluctuations is a specific feature of hydrocarbon-oxidizing bacteriocenoses in oil-producing areas. In soils heavily polluted (up to 10 wt.%) with petroleum products, the average levels of ecologically significant species *R. erythropolis*, *R. globerulus*, *R. opacus*, *R. rhodochrous*, and *R. ruber* are 10^4 – 10^5 cells/g of soil, thus proving their role in the natural biodegradation of petroleum hydrocarbons [25][26][27]. The isolated strains are characterized by emulsifying abilities and biodegradative activities, not only towards aliphatic and aromatic hydrocarbons, and petroleum products, but also towards other recalcitrant and toxic pollutants—heterocycles, oxygenated and halogenated compounds, nitroaromatics, and organochlorine pesticides. They tolerate high (100–250 mM or more) concentrations of toxic metals and metalloids, and organic solvents (from 20 to 80 vol.%). The strains are active in a wide range of temperatures (from 4–15 to 40 °C and above), acidity (pH from 2.0 to 9.0), and humidity (from 15 to 50%), and are able to grow at high (2–6%) salt concentrations [14][20][26][28][29][30]. These *Rhodococcus* strains are the core of the Regional Specialised Collection of Alkanotrophic Microorganisms (acronym IEGM, available online at: <http://www.iegmc.ru> (accessed on 20 July 2021)). The collection has been recognized by the Center for Collective Use (CKP_480868) and included in the National Research Facilities Registry of the Russian Federation [31][32]. The compiled fund of non-pathogenic strains of rhodococci is a helpful resource for identifying novel bioproducers of valuable substances, and biodegraders and biotransformers of complex organic compounds. *Rhodococcus* strains with active oxygenase enzymes are promising candidates for biotechnological processes, such as biodegradation of toxic pollutants and bioremediation of contaminated areas.

In this regard, there is a pressing need for new knowledge on universal and specific features of *Rhodococcus*, particularly those with induced oxygenase enzyme complexes, and new facts about their interaction with xenobiotic compounds. These facts would provide a more fundamental understanding of the role of this actinobacterial group in the functioning of the biosphere, and in removing or decreasing toxic components under the conditions of a destabilized environment. Finally, these species create prerequisites and opportunities for developing advanced biotechnologies of neutralization or efficient reuse of industrial wastes. Rhodococci are relatively new objects of environmental and industrial biotechnologies. Their metabolic potential for biodegradation and inactivation of complex pollutants, in addition to their mechanisms of stress resistance, are far from being exhausted. However, one should be conscious that some members of this genus are pathogens, and their number is gradually expanding, which clearly limits the practical application of rhodococci [33][34][35][36][37][38].

The range of *Rhodococcus* habitats is vast and diverse: these range from nutrient-rich (human and animal organisms, and plants) to oligotrophic (ground water, snow, and air) environments. Their adaptive traits include

protective capsule-like structures and a lipophilic cell wall; colony dissociation and cellular polymorphism; temporarily dormant cyst-like cells and a low level of endogenous respiration (ensuring survival, e.g., upon prolonged starvation); production of carotenoids and extracellular glycolipids; nitrogen fixation in the presence of hydrocarbons; oligo- and psychrotrophy; acido-, alkalo-, halo-, xero-, thermo-, and osmotolerance; cell adhesion; and colonization of surfaces. Such a diversity of adaptive traits allows *Rhodococcus* accommodation in soil and aquatic environments, and possibly drove the appearance of epidemic variants in soil (water) and pathogenization of free-living forms. In extreme conditions of the polluted environment, rhodococci, as true saprophytic Gram-positive bacteria, are able to change their survival strategy in a manner that begins to exhibit traits of antagonism and pathogenicity [22][35].

2. Adaptive Cell Modifications of Rhodococci Exposed to Hydrocarbons and Other Environmental Pollutants

Rhodococci adapt to hydrophobic pollutants generally by forming separate multicellular aggregates (**Figure 1**). For example, when rhodococci were grown in the presence of liquid *n*-alkanes, planktonic micro-sized (25–70 μm in diameter) cell aggregates (microcolonies) of an elongated or rounded shape consisting of viable cells were formed during the first day (**Figure 1A,B**). On days 3–4, macroscopic compact multicellular (biofilm) formations (**Figure 1C**), or mucosal floccular strands (flocks) up to 1 cm in size diffusely located throughout the entire volume of the medium were observed. The spontaneous formation of biofilm clusters (cell aggregates, microcolonies) in the form of dense granules (up to 5 mm in diameter) seen by the naked eye, floating freely in the medium, and remaining until the end of the experiment, reduced the number of suspended cells in the culture broth (**Figure 1D**). By further self-immobilization, larger mushroom-like aggregates with a uniform structure passively floating in the liquid nutrient medium were formed (**Figure 1E,F**). In these cell clusters, the spatial arrangement of cells usually follows the rule of minimum diffusion distance, which ensures the fastest mass transfer between cells. Adhesion forces act at a distance of $<20\text{ nm}$ [39].

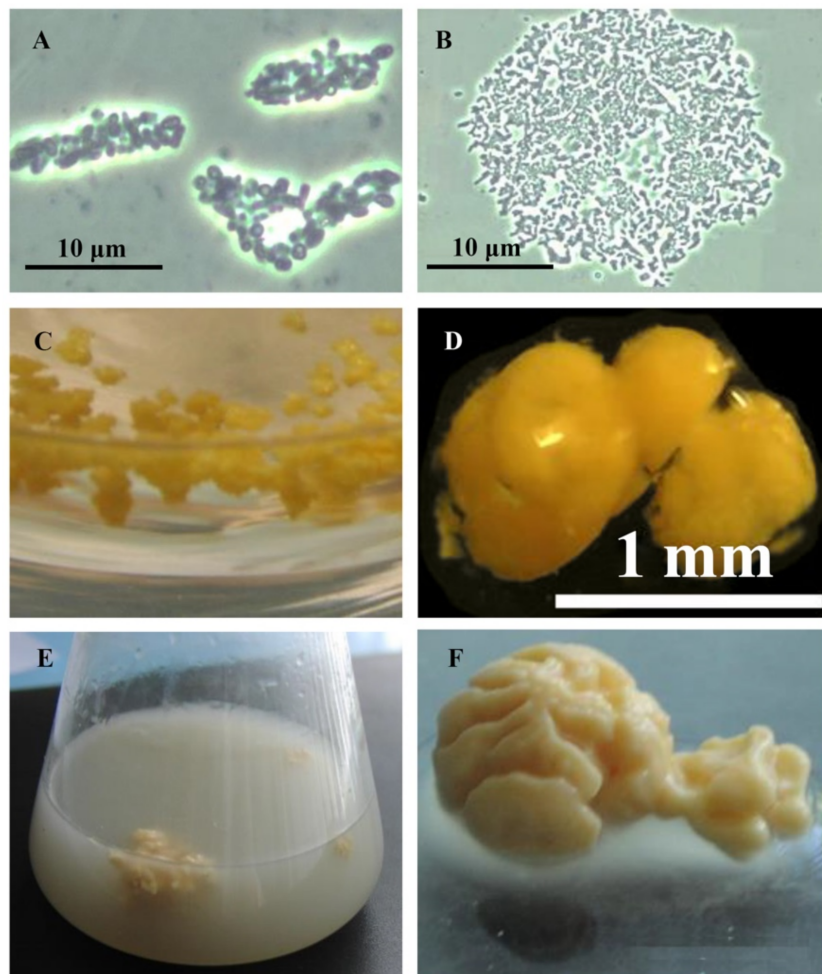


Figure 1. Cell aggregation of *R. ruber* IEGM 326 (A–D) and *R. erythropolis* IEGM 270 (E,F) grown in a mineral salt medium in the presence of 1 vol.% *n*-hexadecane. (A,B)—oblong (A) and rounded (B) cell microaggregates; (C,D)—microbial granules (macrocolonies); (E,F)—isolated cell aggregates.

Aggregation is an effective phenotypic adaptation that allows rhodococci to grow successfully in suboptimal environments. This is one of the factors related to bacterial persistence and pathogenicity. Such a “cooperative cell system” provides the coordinated functioning of numerous associated cells and allows the population to adapt and grow in “harsh” conditions, in which individual cells are not able to reproduce and biodegrade pollutants.

The cell aggregation and the ability to form bulky “oversized” morphotypes, including the presence in the life cycle of “inedible” large branching threadlike cells (greater than the size of a prey for a potential predator), furnish the *Rhodococcus* population with the protection from a range of predators and parasites, such as microbivorous free-living protists (amoebae, flagellates, and ciliates) and bacteriophages [40]. Issues concerning the experimental study of the ecological interactions between bacteria and protozoa, and specific strategies of rhodococci to mitigate the risk of predation by protozoa in soil, freshwater, and marine ecosystems, are still subject to detailed consideration [41][42]. Future research should focus on the complex role of protists and the reduced vulnerability of rhodococci to ecologically relevant species in planktonic microbial communities.

Pronounced heteromorphism, morphogenetic alterations of vegetative cells, a complex development cycle of *Rhodococcus*, and finally, the rigid cell wall structure, are clearly relevant to adaptation. The advantages of these attributes for survival are obvious and can be considered as mechanisms of successful adaptation that determine the stability of *Rhodococcus* populations under variable environmental conditions.

Exposed to ecotoxicants, rhodococci can vary the fatty acid composition of membrane lipids, including mycolic acids and phospholipids, to maintain the level of viscosity of their membranes in the liquid-crystalline state [43][44]. Lipids are one of the few groups of complex organic substances for which the composition can be adequately regulated by the bacterial cell in response to suboptimal growth conditions by changing the structure and relative amount of membrane fatty acids [45]. The key role in determining the fluidity and permeability of *Rhodococcus* cell membranes is due to the composition of fatty acids, which can vary in the length and degree of saturation of the hydrocarbon chains depending on the organic substrate consumed [29][46][47][48].

Rhodococcus are capable of shifting to specific resting (viable but nonculturable, VBNC) forms [11][49] and accumulating large amounts of storage substances, for example, triacylglycerols, esters wax, and polyhydroxyalkanoate, as reservoirs of carbon and chemical energy [50][51][52]. The accumulated neutral lipids are not only a basis for the biosynthesis of mycolic acids and regulation of membrane fluidity, but also a source of endogenous water [7][30], which allows rhodococci to tolerate soil drought and high temperatures [8][12][50][52].

3. Conclusions

Until recently, the image of an “enemy” (less often, a “companion”) dominated in the human–microbe relationships, now it becomes obvious that it is necessary to establish “peaceful coexistence” with this huge world. [53]

Our goal is to highlight the structural, physiological, and biochemical features of a metabolically versatile group of nocardioform bacteria—representatives of the genus *Rhodococcus*, which are well-known biodegraders of hydrocarbons and other lipophilic organic compounds. These bacteria occupy one of the dominant positions in anthropogenically disturbed biotopes, and participate in their attenuation and restoration. The relative simplicity of the *Rhodococcus* cell structures is in harmony with the amazing perfection of their biological organization, and with their ability to form peculiar cellular adaptations having deep impacts primarily on cytology and physiology of rhodococci.

These materials substantiate the idea that the adaptive reactions of rhodococci to the negative effects of ecotoxicants are complex. In the presence of ecotoxicants, the developing *Rhodococcus* population changes smoothly towards the formation of more stable forms adapted to new stressful conditions. In this state, *Rhodococcus* cells are characterized by significant universal morphological changes. The discovered natural means of maintaining constant intracellular conditions in rhodococci exposed to various pollutants are considered to be mechanisms of their adaptation to the changing environment. They provide an improved tolerance of rhodococci to xenobiotics and the ability to change their survival strategy, and show signs of pathogenicity. The high competitiveness and survival of *Rhodococcus* species in any environment, in addition to their pathogenic

potential, are determined by the ability of rhodococci to adhere to, aggregate, and colonize surfaces, and to change their lifestyle (from unicellular to multicellular, and from saprotrophic biodegraders to plant pathogens and animal intracellular parasites); the long-term persistence in unfavorable conditions; diauxotrophy; the formation of cyst-like cells and capsule-like structures; the enhanced cell surface hydrophobicity; ubiquity; and the antagonistic activities of some rhodococci. In medicine, the adaptive mechanisms are commonly referred to as “pathogenicity factors”, with adhesins and adhesion being particularly important as the mechanisms that trigger an infectious process.

Amid the pathogenization of saprotrophs under conditions of man-made pollution, the range of potentially dangerous microorganisms with “unprofessional” parasitism is expanding. There is a certain blurring of boundaries between pathogens and non-pathogens, and the idea of “universal” pathogenic factors of microorganisms is becoming more established. Moreover, it becomes increasingly difficult to predict which group of today's saprophytes will join the list of pathogenic agents of disease tomorrow. At present, there is only an accumulation of research data on *Rhodococcus* survival strategies. The mechanisms of possible pathogenization of saprotrophic rhodococci have not been studied at the level of genome functioning and regulation of their metabolism. This has yet to be undertaken using modern genomic and post-genomic technologies with the use of system analysis.

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