International Scholars Journals

African Journal of Ecology and Ecosystems ISSN 2756-3367 Vol. 8 (5), pp. 001-007, May, 2021. Available online at www.internationalscholarsjournals.org © International Scholars Journals

Review

Taxonomy and ecology of antibiotic producing actinomycetes

Mobolaji Felicia Adegboye* and Olubukola Oluranti Babalola

Department of Biological Sciences, Faculty of Agriculture, Science and Technology, North-West University, South Africa.

Accepted 12 October, 2020

The taxonomic and ecological positions of antibiotic producing actinomycetes are an integral part in antimicrobial agents' development program. Comprehensive understanding of the organisms give useful insight on the secondary metabolites been produced by them and other activities carried out by them in their habitat. Criteria for the identification of actinomycetes include morphological, physiological, ecological and molecular characterization. It is vital to identify the organism up to species level, since this will give an indication whether the antimicrobial agent being produced is novel or not. The suborder and habitat also act as pointers for possible secondary metabolites production and confer the need for further exploration.

Key words: Taxonomy, ecology, actinomycetes, antimicrobial agents, characterization.

INTRODUCTION

Actinomycetes are prolific producers of novel antimicrobial agents (Atta et al., 2010). Vast numbers of these antimicrobial agents are discovered from actinomycetes by screening natural habitat such as soils and water bodies (Duraipandiyan et al., 2010; Gallagher et al., 2010; Zotchev, 2011). A wide taxonomic range of actinomycetes have the ability to produce secondary metabolites with biological activities such as antibiotic, antifungal, antiviral, anticancer, enzyme, immuno-suppressant and other industrially useful compounds (Baltz, 2007; Demain and Sanchez, 2009; Kekuda et al., 2010; Naine et al., 2011; Newman and Cragg, 2007). Antibiotics have been isolated from almost all the suborder of actinomycetes. Despite increase in antibiotic resistance to commonly used drugs, there is still a steady supply of novel antimicrobial agents from actinomycetes isolated from the natural environment (Baltz, 2006; Yang et al., 2011).

Taxonomy is the science of biological classification. The basic taxonomic group in microbial taxonomy is the species. Taxonomic characterization of antibiotic producing actinomycetes is a very important aspect in screening for novel antibiotic (Van Hop et al., 2011). This provides informative insight about the organism, possible kind of secondary metabolite and whether the metabolite is new or not (Labeda, 1987). Major characteristics used in taxonomy for the classification and identification of micro-organisms are morphological, physiological, ecological and molecular characteristics (Willey et al., 2010). Many novel actinomycetes species have been characterized and named, and secondary metabolites extracted from them using various techniques (Kim et al., 2011; Zotchev, 2011). Actinomycetes are phylo-genetically grouped as gram-positive bacteria with high guanine + cytosine in their DNA. Actinomycetes belong to the order, actinomycetales comprising of 14 suborders, 49 families, and over 140 genera (Wikipedia, 2011).

Majority of actinomycetes are free living organisms that are widely distributed in nature. They are found in both aquatic and terrestrial habitat. These bacteria have high mechanisms of survival in adverse environment (Macagnan et al., 2006). The use of molecular techni-ques to study microbial diversity has brought a great advancement to microbial ecology, making it possible to determine the natural microbial population especially, in the soil (Alam et al., 2010; Hirsch et al., 2010). One of the

*Corresponding author. E-mail: adegboye.bolaji@yahoo.com, 23229926@nwu.ac.za. Tel: +27183892627. Fax: +27183892134.

goals of ecology is to study the distribution and biodiversity of microbes in various climate and natural habitat. Actinomycetes population have been identified as one of the prominent group of soil microbes which differ with soil type, soil pH, geographical location and climatic condition (Arifuzzaman et al., 2010). The characterization of these microbes is as important as studying their existence in the natural environments (Hirsch et al., 2010). Actinomycetes play a vital role in the soil such as mineralization of organic matters, immobilization of nutrients, antibiosis and production of plant promoters (Anderson et al., 2011; Sonia et al., 2011).

This review focuses on the taxonomy and ecology of antibiotic producing actinomycetes. It is essential to understand the taxonomy and ecology of secondary metabolites producing actinomycetes to facilitate the exploration of the different strains for biotechnology.

TAXONOMY OF ANTIBIOTIC PRODUCING ACTINOMYCETES

Taxonomy is an integral aspect of science and also important in the screening for novel organisms with the ability to produce secondary metabolites that can be of valuable use. A purposeful search for novel antibiotic will be worthwhile if there is a good knowledge about the species that is producing them (Labeda, 1987). Actinomycetes taxonomy was previously based on morphology, which is inadequate in differentiating between different species of many genera. The use of phylogenetic and molecular evolutionary approaches has greatly helped the classification methods (Babalola et al., 2009; Hozzein and Goodfellow, 2011). Uncultivable or not easily cultivated actinomycetes can now be identified from environmental samples due to the advent of metagenomics (Hirsch et al., 2010; Mincer et al., 2005). Some organisms that are erroneously placed in inappropriate group are now classified appropriately due to the advent of molecular techniques (Zhi et al., 2009). Phylogenies and species identification are now commonly derived from 16S rRNA and the use of polymerase chain reactions (PCR) for sequence analyses (Wood et al., 2007; Zhi et al., 2009).

Taxonomic characterization of antibiotic producing actinomycetes is a tremendously significant step in screening for novel antibiotics (Labeda, 1987). Actinomycetes exhibits considerable physiological and biochemical diversity, the order is diverse in terms of morphology, phylogeny and chemotaxonomy (Kekuda et al., 2010). This group was initially classified based on their branching of filamentous morphology which occurs during the growth cycle (Willey et al., 2010). Thus, due to the presence of the filamentous forms which branches out, these organisms were wrongly classified as fungi for many years before they were rightly placed in the bacteria kingdom (Madigan et al., 2009). Certain criteria are used for the classification and identification up to the species level; these include growth on different media, mycelia pigment, cell wall composition, utilization of carbon and nitrogen sources, production of spores, and molecular % of G + C of DNA (Willey et al., 2010). Recent phylogenetic and molecular techniques including 16S rRNA analysis and DNA-DNA hybridization are commonly used (Hirsch et al., 2010; Ventura et al., 2007).

Actinomycetes are morphologically diverse ranging from rod to coccoid, fragmenting hyphal forms to those with a highly differentiated branched mycelium (Trujillo, 2001). Many of these bacteria also produce external spores. The cell wall composition of actinomycetes is of significant taxonomic value which differs among the different suborder (Berd, 1973). There are four types of cell wall distinguished based on the characteristics of peptidoglycan composition and structure (Willey et al., 2010). These characteristics are: the type of amino acids in tetrapeptide side chain position 3, the presence of glycine in interpeptide bridges, and peptidoglycan sugar content (Willey et al., 2010). Cell extracts of action-mycetes with wall type II, III, and IV also contain characteristic sugars that are useful in identification. Some other taxonomically important features are the cellular morphology, colour of mycelia and sporangia, the surface features and arrangement of conidiospores, the presence of high G + C content in DNA, the phospholipids composition of cell membranes and heat resistant spores (Willey et al., 2010). Modern techniques are applied to actinomycetes taxonomy; comparisons of the 16S rRNA sequences have proven valuable (Zhi et al., 2009). The pattern of 16S rRNA signatures consists of nucleotides at positions 688: 699 (G–C), 701 (C), 823: 877 (G–C) and 1060: 1197 (U–A) (Zhi et al., 2009). Based on the molecular and chemical composition data, the order actinomycetales is grouped into 14 suborders (Wikipedia, 2011). These suborders include: Actinomycineae, Actinopolysporineae, Catenulisporineae, Corynebacterineae, Frankineae, Glycomycineae, Jiangellineae, Kineosporineae, Micrococineae, Micromonosporineae, Propionibacterineae, Pseudonocardineae, Streptomycineae and Streptosporangineae (Euzéby, 1997) and some of them are explained as follows:

Actinomycineae

The genera, *Actinobaculum*, *Actinomyces*, *Arcanobacterium*, *Falcivibrio*, *Mobiluncus*, *Trueperella* and *Varibaculum* are located in this suborder (Euzéby, 1997). Most genera in this suborder have irregular shape, fragmenting filaments without aerial hyphae and spores. They are gram-positive rods with aerobic anaerobic or facultative metabolism (Willey et al., 2010). Their rods may be straight or slightly curved and usually have

swellings, club shapes or other deviation from normal rod-shaped morphology (Trujillo, 2001). The cell wall compositions contain lysine but not diaminopimelic acid or glycine (Sumbali and Mehrotra, 2009). The 16S rRNA nucleotide signature is at position 127: 234 (R–U), 598: 640 (Y–G), 828 (R), 829: 857 (G–C), 832: 854 (G–Y), 1229 (C–G) and 986: 1219 (A–U) (Zhi et al., 2009). They play important ecological role by producing enzymes that help degrade organic matter in the soil such as lignin and chitin. They also help in the formation of compost (Shi et al., 2011).

Streptomycineae

The suborder, *Streptomycineae* has only one family, Streptomycetaceae, and ten genera including *Actinopycnidium*, *Actinosporangium*, *Chainia*, *Elytrosporangium*, *Kitasatoa*, *Kitasatospora*, *Microellobosporia*, *Streptacidiphilus*, *Streptomyces* and *Streptoverticillium* (Euzéby, 1997). The most important of these genera is *Streptomyces*. Bacteria in these genera have aerial hyphae that divides in a single plane to form chains of 3 to 50 or non-motile conidiospores with surface texture ranging from smooth to spiny and warty (Willey et al., 2010). All have a type 1 cell wall and G + C content of around 69 to 78 mol % (Farris et al., 2011). The pattern of 16S rRNA signatures consists of nucleotides at positions 127: 234 (G to C), 449 (A), 672: 734 (C–G), 950: 1231 (U–G), 952: 1229 (U–A), 955: 1225 (C–G), 965 (C), 986: 1219 (A–U) and 1362 (C) (Zhi et al., 2009).

This suborder is very important both ecologically and medically (Farris et al., 2011). The natural habitat of most genera in this suborder is the soil, where they constitute from 1 to 20% of the culturable population (Trujillo, 2001). The odour of the moist earth is largely the result of the *Streptomyces* production of volatile substances such as geosmin (Jiang et al., 2007). They play a major role in mineralization and immobilization of soil nutrients (Sonia et al., 2011). They are flexible nutritionally and can aerobically degrade resistant substances such as pectin, lignin, chitin, keratin, latex and aromatic compounds (Shi et al., 2011). *Streptomyces* are best known for their synthesis of a vast array of antibiotics, some of which are useful in medicine and agriculture (Watve et al., 2001).

Corynebacterineae

This suborder contains 7 families with several genera including *Amycolicicoccus*, *Bacterionema*, *Caseobacter*, *Corynebacterium*, *Dietzia*, *Gordonia*, *Micropolyspora*, *Millisia*, *Mycobacterium*, *Nocardia*, *Rhodococcus*, *Segniliparus*, *Skermania*, *Smaragdicoccus*, *Tomitella*, *Tsukamurella*, *Turi* and *Williamsia* (Euzéby, 1997). The most important ones are *Corynebacterium*, *Mycobac-terium* and *Nocardia*. This suborder is composed of aerobic and facultative, catalase positive, straight to slightly curved rods or filamentous rods. Corynebacterineae are characterized by an unusual cell wall structure, having peptidoglycan with meso-diaminopimelic acids and no peptide interbridge in the cell wall (Van Hop et al., 2011). The wall usually contains carbohydrate composed of arabinose, galactose lipid and mycolic acids, which are usually present in different composition depending on the genera. They are characterized by the presence of mycolic acids. Although, some species are non pathogenic, many are plant and animal pathogens (Pelczar et al., 2006). They have about 64 to 74 mol % G + C content in their DNA. The pattern of 16S rRNA signatures consists of nucleotides at positions 127: 234 (G–Y), 564 (C), 672: 734 (U–G), 833: 853 (U–G), 952: 1229 (U–A) and 986: 1219 (U–A) (Zhi et al., 2009).

Members of this suborder are mostly soil inhabitant and are good survivors on harsh environment because of this attribute they are found in a wide range of environmental niche. They play an important role in bioremediation of heavily oil contaminated environment due to their ability to utilize diverse substrates (Shen et al., 2008). Some genera like *Rhodococcus*, *Gordonia* and *Mycobacterium* also play active roles in the mineralization of polycyclic aromatic hydrocarbons (Uyttebroek et al., 2006). The antibiotic, griseusin was isolated from this family (Gandhimathi et al., 2007).

Micrococcineae

The suborder *Micrococcineae* has 17 families and a wide variety of genera. The suborder contains the families, Beutenbergiaceae, Bogoriellaceae, Brevibacteriaceae, Cellulomonadaceae,Demequinaceae,Dermabacteraceae, Dermacoccaceae, Dermatophilaceae, Intrasporangiaceae, Jonesiaceae, Microbacteriaceae, Micrococcaceae, Promicromonosporaceae, Rarobacteraceae, Sanguibacteraceae and Yaniellaceae (Euzéby, 1997). The two best-known genera are *Micrococcus* and *Arthrobacter*. This suborder contains aerobic, catalase positive, cocci or rods and usually non-motile. The peptidoglycan layer of the cell wall contains lysine. They have about 59 to 70 mol % G + C content (Willey et al., 2010). The pattern of 16S rRNA signatures consists of nucleotides at positions 127: 234 (A–U), 598: 640 (U–G), 657: 749 (U–A), 953: 1228 (G–C), 986: 1219 (A–U), 987: 1218 (A–U) and 1362 (A) (Zhi et al., 2009).

They are widespread in soil, water and on mammalian skin. This suborder is unusually flexible nutritionally and can even degrade some herbicides and pesticides; it is probably important in the mineralization and assimilation of organic molecules (Matsui et al., 2009; Nawel et al., 2011; Viamajala et al., 2007).

Micromonosporineae

This suborder contains only one family Micromonosporaceae with up to thirty genera. The sub-order contains genera like *Actnoplanes, Catenuloplanes*,

Couchioplanes, *Dactylosporangium*, *Micromonospora*, *Pilimelia, Salinispora* and *Verrucosispora* (Euzéby, 1997). They are aerobic like most actinomycetes and their peptidoglycan contain meso-diaminopimelic acid (DAP), glycine, arabinose and xylose. They have an extensive substrate mycelium and are wall type IID. Often times, the hyphae are highly coloured and diffusible pigments may be produced. Condiospores are usually formed within a sporangium raised above the surface of the substratum at the end of special hyphae called a "sporangiosphore" (Willey et al., 2010). The spores can be either motile or non-motile. The G + C content is about 72 to 73 mol %. The pattern of 16S rRNA signatures consists of nucleotides at positions 127: 234 (A–U), 209 (G), 534 (G), 831: 855 (U–G), 832: 854 (G–Y), 833: 853 (U–G), 840: 846 (Y–G), 845 (G), 955: 1225 (A–U), 986:1219 (U–A) and 987: 1218 (G–C) (Zhi et al., 2009).

They are widely distributed in nature; growing in almost all the soil habitat ranging from forest litter to beach sand. Due to their ability to produce hydrolytic enzymes like xylanases and chitinases, they are able to degrade a wide range of organic matter in their natural habitat. Members of this suborder also help in nitrogen fixation (Hirsch and Valdés, 2010).

Propionibacteriaceae

This suborder contains two families and 25 genera including *Aestuariimicrobium*, *Actinopolymorpha*, *Auraticoccus*, *Luteococcus*, *Nocardioides*, *Propionibacterium* and *Thermasporomyces*. The most important genus is *Propionibacterium*, which usually catalase positive, contains pleomorphic, non-motile and non-sporing rods that are often club-shaped with one end tapered and the other end rounded (Wiley et al., 2010). Members of the family have cell wall peptidoglycans including LL-diaminopimelic acid (DAP), meso-DAP or lysine as the diagnostic diamino acid depending on the genus (Jung et al., 2007). The genus if facultative anaerobic or aerotolerant lactate and sugars are fermented to produce large qualities of propionic and acetic acids, and carbon (IV) oxide (Willey et al., 2010). The G + C content varies from 53 to 67 mol %. The pattern of 16S rRNA signatures consists of nucleotides at positions 127: 234 (A–U), 598: 640 (U–A), 657: 749 (G–C), 828 (U), 829: 851 (A–C), 832: 854 (U–C), 833: 853 (G–U), 952:1229 (C–G) and 986:1219 (U–A) (Zhi et al., 2009).

The genus is found growing on the skin and digestive tract of animals and in the diary products such as cheese (Sumbali and Mehrotra, 2009).

Streptosporangineae

The suborder *Streptosporangineae* contains three families and 23 genera including *Actinoallomurus*, *Actinomadura*, *Microbispora*, *Microtetraspora*, *Nonomuraea*, *Nocardiopsis*, *Planobispora*, *Planomonospora*, *Planotetraspora*, *Sphaerisporangium*, *Spirillospora*, *Streptomonospora*, *Streptosporangium*, *Thermomonospora* and *Thermopolyspora*. They have type III cell walls containing meso-diaminopimelic acid and whole cell hydrolysate contains madurose and galactose. Their G + C content is about 64 to 74 mol %. Aerial mycelia bear pairs of short chains of spores and the substrate mycelium is branched. Some genera form sporangia spores are not heat resistant (Wiley et al., 2010). This suborder contains some thermophiles that are being isolated from high temperature habitat such as compost piles and hay. It can grow at 40 to 48°C (Wiley et al., 2010). The pattern of 16S rRNA signature consists of nucleotides at positions 127: 234 (A–U), 829: 857 (G–C), 830: 856 (G– C), 953:1228 (U–A), 950:1231 (U–A), 955:1225 (C–G), 986:1219 (A–U) and 987:1218 (A–U) (Shi et al., 2011).

Frankineae

The suborder contains six families and twelve genera including *Acidothermus*, *Cryptosporangium*, *Fodinicola*, *Frankia*, *Blastococcus*, *Geodermatophilus*, *Modestobacter*, *Humicoccus*, *Nakamurella*, *Saxeibacter* and *Sporichthya* (Euzéby, 1997). They are aerobic, catalase positive with type III cell walls containing sugars like glucose, xylose and galactose, although, the cell extract sugar patterns differs among the different genera (Lee, 2011). They have motile sporangiospores in a sporogenous body. The G + C content varies from 57 to 75 mol %. The pattern of 16S rRNA signatures consists of nucleotides at positions 184:193 (A–C), 195 (A), 196 (U), 582: 758 (U–A), 601: 637 (G–U), 602: 636 (C–G), 841 (C), 952:1229 (U–A), 986:1219 (A–U), 1059:1198 (C–G) and 1308:1329 (C–G) (Zhi et al., 2009).

Members of this suborder have been isolated from various habitats such as rhizosphere, hot springs, activated sludge and geographically diverse soils (Carlsohn et al., 2008). They are involved in nitrogen fixation in association with non-leguminous plants

ECOLOGY OF ANTIBIOTIC PRODUCING ACTINOMYCETES

Microbial diversity is a substantial leading edge and prospective goldmine for biotechnology industry because it offers countless of secondary metabolites to probe for enzymes, antibiotics, antioxidant, cytotoxic and so many other useful substances (Gurung et al., 2009; Singh and Pelaez, 2008; Williams, 2009). The actinomycetes occur in vast diversity of habitat either natural or artificial, growing on different kinds of substrate. The diversity of actinomycetes is of exceptional impact in several areas of pharmaceutical, medicine and agriculture, particularly, in antibiotic production (Blodgett et al., 2008). Actinomycetes are ubiquitous and have been isolated from various locations, in the soil, fresh water, marine,

Table 1. Examples of some rhizospheric actinomycetes and their functions to plants.

Rhizospheric actinomycetes	Function	Plant species	References
Micromonospora endolithica	Phosphate solubilization to promote plant growth	Bean (*Phaseolus vulgaris* L.)	(El-Tarabily et al., 2008).
Streptomyces griseus	Protection against damping off disease caused by *Pythium ultimum*	Wheat (*Triticum spp*.)	(Hamdali et al., 2008).
Frankia species	Biological fixation of nitrogen	Actinorhizal plant (*Casuarina equisetifolia*)	(Rascio et al., 2008).
Norcardia levis	Biological control of F*usarium oxysporum* wilt disease	Sorghum (*Sorghum bicolor)*	(Kavitha et al., 2010).
Streptomyces species	Act as biocontrol against *Rhizoctonia solani*	Tomato (*Solanum lycopersicum*)	(Patil et al., 2011)
Streptomyces species	Bioremediation of contaminated soil	Maize (*Zea mays*)	(Benimeli et al., 2008).

hot spring, mining sites, and also in extreme environments.

Actinomycetes as soil inhabitant

Soil is a unity entity that inhabits varieties of micro-organisms and the microbial community is an integral part of the soil. Actinomycetes are primarily soil inhabitants and are also very widely distributed in nature (Babalola et al., 2009; Gurung et al., 2009). They are also well known as soil saprophytes and are responsible for the distinctive earthy odour of freshly ploughed soil due to the production of geosmin. The most dominant actinomycetes in soil is the genus *Streptomyces* although, others like *Norcardia, Microbispora*, *Micromonospora*, *Actinomyces*, *Actinoplanes* and *Streptosporangium* have also been isolated from the soil. The number and variety of actinomycetes present in any soil sample would be significantly influenced by geographical location, soil temperature, soil type, soil pH, organic matter content, agricultural activities, aeration, nutrient availability, moisture content and soil vegetation (Arifuzzaman et al., 2010). Actinomycetes have been isolated from diverse soil types and locations such as arid, tropical forest, mining, cave, swamp, desert and savannah. They are particularly abundant in slightly alkaline soils rich in organic matters and produce several structurally diverse secondary metabolites of pharmaceutical and agricultural importance.

Actinomycetes play an important ecological role in the recycling and mineralization of nutrients in the soil. They help to recycle nutrients by degrading vast numbers of organic matter in the soil and are found most common in compost. They act as plant growth promoters by helping in nitrogen fixation, solubilization of nutrients, immobilization of nutrients, siderophores production, biological control and soil structure maintenance (Kekuda et al., 2010; Macagnan et al., 2008; Rascio et al., 2008; Vargas Gil et al., 2009). Actinomycetes are of great practical importance in nature and seem to be ultimately involved in soil ecology (Van Hop et al., 2011).

Actinomycetes as rhizobacteria

Rhizosphere is defined as the soil ecological zone surrounding the roots of growing plants. It is a unique biological niche within the soil environment having high nutrients content and housing numerous and diverse soil microbes. The high nutrient content in the rhizosphere is as a result of sloughed off plant cell (rhizodeposition) and exudates from the roots such as proteins and sugars. The high nutrient content in the rhizosphere makes the microbial load higher than that of the surrounding bulksoil. The bacteria which colonize plant root are called rhizobacteria. They specifically multiply and inhabit the growing plant root system and continue throughout the life span of the plant. A rhizobacterium may form a symbiotic relationship with a plant, for example when the bacterium produces antibiotic that inhibit plant pathogens in exchange for nutrients. Such microbes are also referred to as plant growth promoting rhizobacteria (Compant et al., 2010).

Actinomycetes are one of the prominent soil microbes and they grow in close association with the plant organs. They form thread-like filaments in the soil which give them an advantage in colonizing the rhizosphere effectively. As a rhizobacteria, they influence plant growth, antagonize plant pathogens and makes nutrients available for the plants (Maheshwari and Shimizu, 2011). Actinomycetes are known to be versatile degraders of complex organic matters such as cellulose, lignin, xylan, chitin and other complex polysaccharides (Macagnan et al., 2008). The production of hydrolytic enzymes makes it possible for actinomycetes to break down organic matter in their natural environment (Marsh and Wellington, 2007). Several reports have shown that actinomycetes are one of the important groups of root-colonizing micro-organisms (Franco-Correa et al., 2010; Nimnoi et al., 2010) (Table 1).

CONCLUSION

Actinomycetes play a significant role in the production of antimicrobial agents and other industrial important substances like enzymes. It is essential to have a good knowledge about their taxonomy and ecology for maximum exploration, since they are of great use for economic and industrial development. In soil ecology, they are also active in bioremediation, biofertilizer, biocontrol and as plant growth promoters, making them indispensable in agricultural practice. Although, a great work has been carried out on actinomycetes, more comprehensive studies are still needed in the area of taxonomy and ecology. This will help to predict the productivity of the members of this order and possible exploitation.

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