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A changing view of *Pseudomonas* from being human pathogen, coming to phytopathogen and finally as biocontrol agent

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Abstract

Pseudomonas is one of the utmost learn species of bacteria. It was first identified at the end of 19th century by Migula as Gram-negative, rod-shaped and polar-flagellated bacteria. This followed the description of genus *Pseudomonas* in wide manner. With the advancement of new technologies detail study regarding the morphology and physiology of these bacteria was made possible, whereas the morphological characteristics of *Pseudomonas* are similar to many bacterial genera and thus are of little value in the positive identification of members of the genus. To discriminate it from other similar genera advanced nucleic acid-based methods are utilized which disclose taxonomic relationships among different bacterial species including *Pseudomonas*. Variability among *Pseudomonas* draw attention for vast research interest in this genus. So, this review focuses on the three most explored species of *Pseudomonas* naming *P. aeruginosa*: a human pathogen showing enhanced antibiotic resistance, *Pseudomonas syringae*: most destructive phytopathogen and *P. fluorescens*: an efficient biocontrol agent to understand the morphology, biochemical and different mechanisms adapted by the *Pseudomonas* which ultimately will create an idea of its diversity.

Keywords: *Pseudomonas*, human pathogen, Phytopathogen, Biocontrol agent

Introduction

Among all bacteria the genus which ranked first for its destructive nature is *Pseudomonas*. It is basically Gram-negative in nature and belongs to Gammaproteobacteria, under family Pseudomonadaceae. It includes diverse population containing 191 validly described species. (Euzebey, J. P., 1997) [15] Due to its metabolic variability it can easily colonize a wide range of niches where as they can be easily cultured in the laboratories (Madigan, M. *et al.*, 2005) [34]. Between its all the species most studied species are *P. aeruginosa* (an opportunistic human pathogen), *P. syringae*, the soil bacterium (the plant pathogen) and *P. fluorescens* (biocontrol agent). The generic name was given by Walter Migula in 1894 [40] and its nature as genus defining specific characteristics like Gram-negative, rod-shaped and polar flagellation in 1900. (Migula, W., 1894 & Migula, W., 1900) [40, 41]. *Pseudomonas* was initially classified at the end of 19th century. It appeared in seventh edition of Bergey's Manual of Systematic Bacteriology denoted as greek language as pseudos meaning "false" and monas meaning "a single unit", thus its name refer as false unit. Migula consider it as a nonflagellated protest (Palleroni, N. J., 2010) [46]. In present era 16S rRNA sequence analysis have been used which lead to redefinition of the bacterial species. (Anzai, Y. *et al.*, 2000) [1]. Thus, broad genus *Pseudomonas* also consist strains earlier classified in the genera Chryseomonas and Flavimonas. (Yabuuchi, E. *et al.*, 1992) [61] Where as some strains previously included in the genus *Pseudomonas* are now classified in the genera Burkholderia and Ralstonia. (Yabuuchi, E., *et al.* 1992 & Yabuuchi, E., *et al.* 1995) [61, 62]. In this era of molecular studies *pseudomonas* is not too far including its complete genome sequencing which has been done in 2000 many of its has been too sequenced like including *P. aeruginosa* strains PAO1 (2000), *P. putida* KT2440 (2002), *P. protegens* Pf-5 (2005), *P. syringae* pathovar tomato DC3000 (2003), *P. syringae* pathovar syringae B728a (2005), *P. syringae* pathovar phaseolicola 1448A (2005), *P. fluorescens* Pf0-1, and *P. entomophila* L48 (Cornelis, P., 2008) [9].

Nature: *Pseudomonas* is gram negative rod shaped flagellated bacteria which are basically aerobic and spore forming. It shows positive response towards catalase and oxidase reaction. In iron deficient environment it secrete a secondary metabolite pyoverdine which is yellow in color and act as siderophore (Meyer, J. M *et al.*, 2002) [39]. It also poses a special feature of Quorum Sensing systems due to its ability to synthesize and perceive chemicals of various

property and origin secreted by other bacteria. These are basically considered as messages released in different environment of diverse origins. This system are mostly connected with additional regulons, Eventually leading to diverse phenotypes (Venturi, V., 2006) [34]. For instance, *Pseudomonas putida* secrete a chemical cyclic lipopeptide surfactants naming putisolvin I and II which are under the power of QS and disrupt biofilms (Kuiper, I., 2004 & Kruijt, M., 2009) [30, 29]. Some other putisolvin also inhibit growth of some fungal pathogen like *Phytophthora capsici*, *Botrytis cinerea* and *Rhizoctonia solani* as it exhibit lytic activity against the zoospores (Kruijt, M., 2009) [29]. Thus these chemicals and their resulting interactions like modification of diversity would contribute to total composition of plant microbiome. It was demonstrated that QS play role in the production of an *N*-acyl-L-homoserinylactone (AHL), cyclic dipeptides and their derivative diketopiperazines (DKPs), and the function of DKP is stimulation of lateral roots growth. Thus it can be concluded that Plant growth promoting property of *Pseudomonas* is also under control of QS. (Campos-Garcia, J., 2011) [6]. The present review discusses the three important species of *Pseudomonas* i.e *Pseudomonas aeruginosa*, *P. syringae*, *P. fluorescens*.

***Pseudomonas aeruginosa*:** *Pseudomonas aeruginosa* is mostly isolated from soil and water, and well-known for its nutritional variation and ecological diversity. It is basically an opportunistic human pathogen causing of nosocomial infections and is responsible for persistent infections in immune compromised individuals and for the chronic lung infections of patients with cystic fibrosis (Govan, J. R. *et al.*, 1996) [19]. It also causes serious infections in insects (Jander *et al.*, 2000) [25], nematodes (Mahajan-Miklos S., *et al.*, 1999) [35], and plants (Rahme L. G. *et al.*, 1995; Silo-Suh L. *et al.*, 2002) [49, 51]. The potential of this organism to cause infection is may be due to a set of well-regulated virulence factors and defense mechanisms like multidrug resistance pumps (Chuan-Chuen. R. *et al.*, 2001) [8] and biofilm formation (Costerton J.W. *et al.*, 1999, Singh P.K. *et al.*, 2000; Drenkard E. *et al.*, 2002) [10, 53, 13]. Since formation of film protects bacterial cells from unfavourable environmental conditions (Costerton J.W. *et al.*, 1999) [10] biofilm formation in *P. aeruginosa* occurs through a succession of programmed steps. The first stage of biofilm formation needs flagellar motility and surface attachment by type IV pili-mediated twitching and finally the microcolony aggregation (O'toole, G. A., 1998) [44]. *P. aeruginosa* has two different QS systems named as las and rhl systems; they regulate numerous genes (Pesci E. C. 1999) [48]. To reduce its virulence recent advances has made to restrict the biofilm development (Singh P.K. *et al.*, 2002) [52]. In 2004 Walker *et al* did an experiment to study *P. aeruginosa* pathogenicity and biofilm formation using plant roots as the host. They explored the production antimicrobial compounds from plant roots to secrete antimicrobial compounds into the rhizosphere. They reported that *P. aeruginosa* strains PAO1 and PA14 have the capacity to infect the roots of *Arabidopsis* and sweet basil (*Ocimum basilicum*), in laboratory and soil condition both. Mortality was observed in plants 7 day after inoculation.

***P. fluorescens*:** *Pseudomonas fluorescens* comprises assemblage of nonpathogenic saprophytes that are present in soil, water and plant surface. These are also gram negative, rod-shaped multiple polar flagellated bacterium having

obligate aerobic nature except few strains use NO₃ as an electron acceptor instead of O₂. As the name refer it secretes it a soluble greenish fluorescent pigment called fluorescein in peculiar conditions. The nutritional requirement of these bacteria is very simple and culture wells in media having mineral salts added with numerous carbon sources. (Palleroni. N.J., 1984) [45]. *P. fluorescens* have the potential to behave as biocontrol agent who restricts the plant diseases by defending the seeds and roots from fungal infection. They are also involved in promoting plant growth promotion and decrease the severity of biotic stress (Hoffland E. *et al.* 1996, Wei G. *et al.* 1996) [22, 59]. There are various mechanisms behind it but the important one is the production of various secondary metabolites consisting antibiotics, siderophores and hydrocyanide (O'Sullivan D.J. *et al.*, 1992) [43]. On evaluating the

P. fluorescens B16 genomic library a special set of genes known as pyrroloquinoline quinone (PQQ) biosynthetic genes were observed accountable for betterment of plant health; PQQ has been reported to behave as an antioxidant in plants (Choi, O. *et al.*, 2008) [7]. Role of HCN in the induction of resistance has been reported against several phytopathogenic fungi like *Thielaviopsis basicola* on tobacco (Laville J. *et al.*, 1992 & Voisard, C. *et al.*, 1989) [31, 56], *Septoria tritici*, and *Puccinia recondita* f. sp. *tritici* on wheat (Flaishman, M. A., 1996) [16]. HCN in respiratory chain holds back the terminal cytochrome c oxidase [Knowles, C. J. (1976) [28].] and thus binds to metalloenzymes (Blumer, C., 2000) [5]. An interesting result was observed that siderophore-mediated iron competition by *P. fluorescens* is also beneficial in prevention of human pathogen growth *Escherichia coli* O157:H7 developing on food products [McKellar, M. E. *et al.*, 2003] [37]. Competition for Root Niches and Nutrients is another mechanism which helps in inhibition of other fungal pathogens. For colonization of root bacterial lipopolysaccharides, play a major role particularly the O-antigen chain. In *P. fluorescens* too O-antigenic side chain of PCL1205 has found to be involved in tomato root colonization [Dekkers, L. C. *et al.*, 1998] [12]. Endophytic *P. fluorescens* strain ALEB 7B isolation from *Atractylodes lancea* significantly restricts the growth of *Athelia rolfsii* strain SY4 by producing antibiotics and lytic exoenzymes which eventually compete for spaces and nutrients (Zhou, J. Y. *et al.*, 2014) [63]. ACC deaminase activity of *P. fluorescens* (Blaha, D. *et al.*, 2006) [4] is one of the major feature for biological control as they decrease the quantity of plant aminocyclopropane-1-carboxylic acid deaminase (ACC) left for ethylene synthesis (Glick, B. R. *et al.*, 2005) [18]. Siderophores produced by *P. fluorescens* WCS374 and WCS417 by restricting iron availability triggers ISR. (Leeman, M., 1996) [33]. Phl (2,4-Diacetylphloroglucinol) is formed by *P. fluorescens* CHA0 participate in ISR against *Peronospora parasitica* (Iavicoli, A., 2003) [23]. It was observed by Sarvanakumar and Kavino that green gram plants bacterized with *P. fluorescens* shown enhanced proline content (Sarvanakumar, D., *et al* 2011) [50]. likewise, interaction has been reported between *P. fluorescens* CHA0 and 7NSK2, they were found to trigger an oxidative burst and formation of phytoalexin in grape leaves when inoculated with *Botrytis cinerea* (Verhagen, B. W., 2009) [55]. Another example is combine application of *P. fluorescens* and *T. viride* which leads to accumulation of phenols and activation of PR proteins in coconut palm in comparison to single-microbe-treated and control plants (Karthikeyan, M., 2006) [26].

Pseudomonas syringae: *P. syringae* is one of important member of the genus pseudomonas and on the basis on 16S rRNA analysis, it has been classified under *P. syringae* group. (Anzai, Y. *et al.*, 2000) [11] The name of this pathogen is based after the lilac tree (*Syringa vulgaris*), through which it was isolated first (Kerstens, K. *et al* 1984) [27]. The species *Pseudomonas syringae* causes several major diseases in a broad range of plant species but is very specific towards its host. This specificity towards their host is the origin of grouping *P. syringae* strains into pathovars (pv.). Nearly 50 pathovars have been identified (Gardan, L. *et al.*, 1999) [17], and further each pathovar is again classified into numerous races depending on differential interactions with cultivars of a plant species. *P. syringae* are local infecting, hemibiotrophic pathogen. Which majorly invade upper parts of plants like leaves and fruits. This pathogen has peculiar life cycle including both epiphytic and endophytic phase. In the initials of their life stage they behave as ephyte as land on the plant surface whereas after gaining entrances into plant (apoplast) they act as endophyte (Beattie, G. A. *et al*, 1995, Hirano, S. S. *et al*, 2000 & Melotto, M. *et al.*, 2004) [3, 20, 38]. *Pseudomonas syringae* severely infest the plant species through different mechanisms like their capability to invade plants with the help of flagella and pili by which they easily swim towards their target host. (Ichinose, Y., *et al.*, 2013) [4]. They consist numerous virulence factors known as type III secretion system (T3SS) effector proteins. These help in formation of disease symptom and change in immune of host which further help in causing infection. In *P. syringae* the major family of

T3SS effectors is the *hrp* gene cluster which codes for the Hrp secretion apparatus (Ichinose, Y., *et al.*, 2013) [4] another mechanism is the production of phytotoxins which harm the plant thus suppressing the host immune system. Interesting characteristics of *P. syringae* surface frost damage in plants (Hirano, S. S, 1995) [20] when exposed to the environment. *P. syringae* leads freezing of water at temperatures -1.8°C (28.8°F), (Maki, L. R., *et al.*, 1974) [36] but in some strains it also causes ice nucleation at lower temperatures like down to -8°C (Lee, R.E. *et al.*, 1995) [32]. This freezing is the reason behind the injuries in the epithelia and makes the nutrients available to the bacteria which underlies in the plant tissue. The *ina* (ice nucleation- active) form INA proteins which ultimately participate in ice nucleation. The presence of *P. syringae* could also be observed in the middle of hailstones which suggest that it has certain role in Earth's hydrological cycle. (Palmer & Jason 2011) [47] There are many factors which help in infections as bacteria enter the plant in passive manner thus wounding is the major one. Wound could be mechanical or any due to any biotic or abiotic stress. It predisposes trees to several diseases like blossom blight and bacterial canker (Moore, L. W., 1988) [42]. Plant Dormancy is next factor which facilitates infection. For example the Dormant peach trees have been observed to be higher susceptible to the disease than the non dormant one. (Wilson, E. 1939 & Davis, J. R. *et al.*, 1969) [60, 11]. Coming to soil, it too influences the growth of bacteria by its soil pH, presences of mineral nutrition,

Table 1

Name of pathovar	Host plant
<i>Pseudomonas syringae</i> pv. <i>garcae</i>	Coffee <i>Coffea arabica</i>
<i>Pseudomonas syringae</i> pv. <i>eriobotryae</i>	Loquat <i>Eriobotrya japonica</i>
<i>Pseudomonas syringae</i> pv. <i>tomato</i>	Tomato <i>Lycopersicon esculentum</i>
<i>P. s.</i> pv. <i>aesculi</i>	Horse chestnut <i>Aesculus hippocastanum</i>
<i>P. s.</i> pv. <i>aptata</i>	Beets <i>Beta vulgaris</i>
<i>P. s.</i> pv. <i>atrovaciens</i>	Wheat <i>Triticum aestivum</i>
<i>P. s.</i> pv. <i>dysoxylis</i>	Kohekohe tree <i>Dysoxylum spectabile</i>
<i>P. s.</i> pv. <i>japonica</i>	Barley <i>Hordeum vulgare</i>
<i>P. s.</i> pv. <i>lapsa</i>	Wheat <i>Triticum aestivum</i>
<i>P. s.</i> pv. <i>panici</i>	<i>Panicum</i> grass species
<i>P. s.</i> pv. <i>papulans</i>	Crabapple <i>Malus sylvestris</i> species
<i>P. s.</i> pv. <i>phaseolicola</i>	Beans
<i>P. s.</i> pv. <i>pisi</i>	Pea <i>Pisum sativum</i> .
<i>P. s.</i> pv. <i>syringae</i>	Pome and stone fruits
<i>P. s.</i> pv. <i>glycinea</i>	Soybean <i>Glycine max</i>

Important symptoms caused by *P. syringae* are: A) blast of flower in which flowers and buds converts to brown to black. B) Death of dormant buds, most easily observed on cherries and apricots. C) Leaf spots which finally turns to necrotic, whole young leaves get finally killed D) Discoloration and blackening of leaf veins E) Small Spots and blisters on fruit. F) Dieback of shoot appears). G) Stem cankers at which enlarge with the time eventually leads to girdling of stem. The girdling of stem would cause death of branch or whole plants (Moore, L. W., 1988) [42] The symptoms of *Pseudomonas syringae* propose the involvement of toxin. This toxin has been isolated and chemically characterized. Earlier the toxin was considered to be formed by all virulent strains causing responsible damage to tissue. But by the time it was made clear that production of toxin has poor correlation with the virulence. (Moore, L. W., 1988) [42].

Conclusion

Genus *Pseudomonas* includes a varied group of bacteria consisting a large number of species. On the one hand, *Pseudomonas* has the ability to infect human causing chronic diseases, causing severe economic losses by attacking a number of the plant species in population level but in other hand its one of its species behave as biocontrol agent. It reduces and inhibit the harmful effect of plant pathogens by different ways. They either secrete compounds that directly influence pathogens or encourage development of induced resistance in plants Recently *Pseudomonas* is also used in bioremediation by degrading toxic compounds and solving problems regarding wastes hazardous of environment and humans. Summing up, *Pseudomonas* species and their diversity is very interesting in regard of evolution and still a varied question still to be explored.

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