



Wonders of the Invisible World: *Pseudomonas syringae*, the Ice Maker

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Abstract

This literature review explores the multifaceted role of *Pseudomonas syringae*, a bacterium renowned for its ice-nucleating properties. *Pseudomonas syringae* significantly influences atmospheric processes, agriculture, and various ecosystems. These bacteria, equipped with ice nucleation proteins (INPs), facilitate ice formation at temperatures warmer than the typical freezing point, impacting weather patterns by initiating snow and hail formation. While its ice-nucleating activity can lead to frost damage in agriculture, it is also harnessed for artificial snow production. This review synthesizes findings on the bacterium's characteristics, morphology, physiology, and ecology, drawing from diverse studies. It highlights its widespread presence in various environments, including plant surfaces, water bodies, and atmospheric samples, emphasizing its adaptability and ecological significance. By employing content analysis on secondary data sources, this study provides a comprehensive understanding of *Pseudomonas syringae*'s unique ability to mediate ice formation and its broader implications for environmental balance and biotechnological applications.

Keywords: INA bacteria, *Pseudomonas syringae*, ice formation, InaZ protein

A. Introduction

The wonders of the world are not only limited to magnificent buildings or awe-inspiring natural phenomena but also include invisible things that have a profound impact on life on Earth. Just as ecosystems depend on unseen interactions between species or microscopic biological processes within living organisms, the wonders of the world can also appear in forms

far smaller than we usually notice. Among these invisible wonders is the world of microorganisms.

According to Puspita *et al.* (2024), microorganisms are fundamental in sustaining ecosystem balance and supporting life on Earth. They contribute to key natural processes such as decomposition, nutrient cycling, and the creation of phenomena that sustain the environment. One such microorganism with remarkable abilities is *Pseudomonas syringae*, a bacterium that is capable of forming ice through a specialized protein found on the surface of its cells. This protein acts as the primary trigger for water freezing by accelerating crystallization, enabling ice to form at temperatures above the normal freezing point (Bieber & Borduas-Dedekind, 2024). This unique trait allows *Pseudomonas syringae* to play a critical role in the formation of snow and hail in the atmosphere, significantly impacting weather patterns across different regions.

Beyond its influence on weather, this bacterium also has a profound effect on agriculture. Its ice-forming ability can induce frost, potentially damaging plants by speeding up the freezing of water on the surfaces of leaves. This phenomenon can lead to significant crop losses by reducing agricultural yields (Majorina, *et al.*, 2022). However, humans have also found a way to leverage this bacterium's abilities in industries, particularly in producing artificial snow for winter sports, showing that microorganisms can bring both challenges and benefits to human life.

These ice-nucleating bacteria are not confined to land; they are also present in marine environments. Research has shown that *Pseudomonas syringae*, when carried into the atmosphere, can accelerate cloud formation and increase rainfall, thereby influencing global weather patterns (Hanlon *et al.*, 2023). Additionally, this bacterium is known to initiate freezing at temperatures ranging from -1.8°C to -3.8°C , playing an essential role in atmospheric processes such as the formation of snow and hail (Roeters *et al.*, 2021).

Research into *Pseudomonas syringae* continues to evolve, deepening our understanding of its mechanisms and potential applications in various fields. Its unique ability to form ice in plants also contributes to maintaining the ecological balance through its interaction with host organisms (De Araujo *et al.*, 2019). The presence of this bacterium illustrates that the wonders of the world are not always grand and visible but can also exist in the smallest, invisible forms. Understanding the role of microorganisms like *Pseudomonas syringae* in life provides new insights into how even the tiniest entities contribute to maintaining the delicate balance of nature.

In this review, we discuss current findings related to the morphology, physiology, environmental role, and applied potential of *Pseudomonas syringae*, particularly focusing on its function as an ice-nucleating agent. *Pseudomonas syringae* is a versatile bacterium that has attracted significant attention due to its unique ability to catalyze the formation of ice at temperatures higher than the typical freezing point of water.

B. Literature Review

1. Characteristics of *Pseudomonas syringae* Bacteria

Domain	: Bacteria
Phylum	: Proteobacteria
Class	: Gammaproteobacteria
Order	: Pseudomonadales
Family	: Pseudomonadaceae
Genus	: <i>Pseudomonas</i>
Species	: <i>Pseudomonas syringae</i> (Gomila <i>et al.</i> , 2017)

Pseudomonas syringae is a plant pathogen that causes diseases known as bacterial blight, spots, streaks, and cankers. *Pseudomonas syringae* can enter the host leaf through wounds and stomata, multiply exponentially, and cause disease. Still, it is also found with strains that can survive on the leaf surface for long periods as epiphytes without causing disease symptoms (Clarke *et al.*, 2010). This species exhibits a wide range of virulence factors. *Pseudomonas syringae* has a type III secretion system (T3SS) and its effector repertoire, toxic compounds, exopolysaccharides, ice nucleation activity, cell wall-degrading enzymes, and plant hormones, which makes it a model for phytopathogenic bacteria (Barranquero *et al.*, 2019).

P. syringae triggers the formation of ice that damages plant cells, a special protein called ice nucleation protein (INP) produced by the bacteria. This protein acts as a nucleus for ice crystal formation, allowing the water around the bacteria to freeze at around -2°C to -5°C , higher than the freezing temperature of pure water (-0°C). In plants, this makes them more susceptible to bacterial

infection. Besides being detrimental to plants, this ice-forming ability is also utilized in industry, such as making artificial snow for skiing or climate research. *Pseudomonas syringae* has wide genetic variation, with many strains attacking different types of plants. One well-known strain is *P. syringae* pv. *tomato*, which causes bacterial blotch on tomatoes. Its high adaptability makes this bacterium a serious threat to global agriculture. However, recent research has shown that bacteriophages (viruses that infect bacteria) such as phage D6 can be used as biological control agents to reduce the impact of *P. syringae* infection on crops (Wu et al., 2024).

Pseudomonas syringae bacteria through isolated from leaf litter and found to form ice nuclei with freezing points up to -2°C , a high temperature compared to other ice-forming substances such as pollen, minerals, and some organic particles that form ice nuclei with freezing points of -15°C . This temperature is far from the homogeneous freezing temperature of water, very cold pure water droplets with a diameter of $10\ \mu\text{m}$ freeze in one minute at -38°C . *Pseudomonas syringae* nucleation activation comes from the ice-nucleating protein (INpro) or commonly called *inaZ*. Based on the different aggregate sizes that trigger freezing at temperatures of -2°C , -6°C , and -7°C , each of these is caused by protein-protein interactions and protein ions likely to promote dimerization and aggregation of Inpro and are also sensitive to Ph (Bieber & Borduas-Dedekind, 2024).

2. Morphology of *Pseudomonas syringae* bacteria

Isolation of *Pseudomonas syringae* pv. *Atrofaciens* strains on potato agar medium showed two colony shapes, namely the smooth, shiny S shape with slightly wavy edges, and the rough, matte, and flatter R shape (Butsenko et al., 2020). *P. syringae* colonies are round and convex with a grayish white or brownish white (cream) color (Fauziyah, 2022). Gram staining tests show that this bacterium is Gram-negative with rod-shaped cells with dimensions of around 0.5–1.0 micrometers in width and 1.5–4.0 micrometers in length (Suyono & Farid, 2011) and is red in color (Missa & Anselmus, 2019). The characteristics of *Pseudomonas syringae* include round, smooth, clear colonies with slightly wavy edges, and the ability to produce fluorescent pigments that glow green under UV light (Masnilah et al., 2013).

According to Kutschera et al. (2021), *Pseudomonas syringae* is a Gram-negative bacterium with a complex lipopolysaccharide (LPS) structure on the outer membrane. LPS consists of three main components, namely: (1) Lipid A, which functions as a binder to the outer membrane and maintains its stability; (2) Core oligosaccharide (core-OS), which is divided into inner core-OS (composed of L-glycero-D-manno-heptose and 3-deoxy-D-manno-oct-2-ulosonic acid or Kdo) and outer core-OS, which is more varied with residue content such as L-rhamnose (Rha) and N-acetyl-D-glucosamine (GlcNAc); and (3) O-polysaccharide (OPS), the most distal part that determines serotype specificity between strains. This LPS structure has a high level of phosphorylation in the core-OS as well as the presence of sugars that undergo O-acetylation, which can affect the interaction with the host immune system and increase resistance to attacks by the plant defense system.

3. Physiology of *Pseudomonas syringae* Bacteria

Bacterium *Pseudomonas syringae* as an ice-active bacterium, is often used to facilitate the production of artificial snow in winter sports areas around the world. Ice-forming proteins (INPs) added to the outer cell membrane of ice-active bacteria can induce the formation of ice crystals that are close to the melting point of ice. *Pseudomonas syringae* bacteria use the ice nucleation protein *inaZ* to promote ice nucleation. *InaZ* is a membrane protein located in the outer cell membrane of *Pseudomonas syringae*, where it can interact with the surrounding water layer (Pandey et al., 2016). The special ability of *Pseudomonas syringae* to form efficient IN has been shown to affect the atmosphere. The glaciation of the formation of droplets that make up clouds is an important mechanism that causes precipitation (including hail formation), and is largely determined by IN particles in suspension in the air. Due to the lower vapor pressure above ice crystals than supercooled liquid water, frozen particles can collect water and grow to a considerable size through precipitation in clouds (de Araujo et al., 2019).

Pseudomonas syringae is often found on leaf surfaces and plant tissues. Under certain conditions, especially when the temperature drops, the ice protein produced by this bacterium can cause ice crystals to form on plant tissues, eventually causing wounds. These wounds open the door for the bacteria to infect the inside of the plant and multiply. This shows how *P. syringae* uses the ability to form ice as a strategy to cause disease in plants. In addition, *P. syringae* has also been

found in the atmosphere, such as in clouds, rain, and snow. In the atmosphere, its ability to form ice can trigger water condensation and aid in the formation of rain or snow (Torma et al., 2025). The results of the study have revealed the most abundant INA bacteria that play a role in influencing interfacial water, the hydrological cycle, local and global climate, and vegetation. *Pseudomonas syringae* as an INA bacterium that causes cloud glaciation, snow precipitation, and hail, and cloud formation because it was found that *Pseudomonas syringae* is active against ice and freezes at a temperature of -20°C. The ice-nucleating protein InaZ from *Pseudomonas syringae* adopts a β -helical structure and controls the interfacial water structure, increasing the effectiveness of ice nucleation at low temperatures (Roeters et al., 2021).

4. Ecology of *Pseudomonas syringae* Bacteria

The results of the isolation carried out by Pavankumar et al. (2021) explain that *Pseudomonas* can grow and survive at a temperature of 40°C. The *Pseudomonas syringae* strain has been studied extensively. Strain Lz4W can grow at temperatures between 0 and 30°C, with optimum growth at a temperature of 22°C with a pH for growth ranging from 6-9 (with 8 as the optimal pH) and a salt tolerance limit of 5.8% (w/v) NaCl. with G+C Mol% for strain Lz4W is 64.4. *Pseudomonas syringae* cannot utilize glycine, serine, phenylalanine, L-tyrosine, n-propanol, ethanol, butanol, and polyethylene glycol, but as explained, *Pseudomonas syringae* can utilize most other common carbons such as gentamicin, kanamycin, streptomycin, and tetracycline. This bacterium can form large colonies on the surface of the air on various plant species without causing disease. From the epiphytic phase, this bacterium is spread through aerosols. *Pseudomonas syringae* is one of the few pathogens that spreads to the clouds and is also swept into the air during rain (Morris et al., 2007).

The evolutionary history of the genus *Pseudomonas* hundreds of millions of years ago whose habitat was in aquatic areas without higher plants, and long before the emergence of agriculture (about 10,000 years ago). *Pseudomonas syringae* has been known to regularly have habitats in mountain lakes and rivers, although the population size is only a small fraction (0.1% or less) of the total population cultured in these waters 65,66 (Cindy et al., 2013). *Pseudomonas syringae* bacteria are ubiquitous in natural and artificial environments. *Pseudomonas syringae* has been cultivated from clouds, rain, snow, rivers, and lakes (Hanlon et al., 2023).

This bacterium is unique in that it can form ice cores by producing a special protein that helps water freeze at higher than normal temperatures. In agriculture, this ability is very important because ice crystals formed on the surface of plants can damage plant tissue, creating wounds that make it easier for bacteria to enter and infect the inside of the plant. This infection causes various symptoms such as necrotic spots on leaves, black spots on fruits, wilting of plant shoots, and even death of branches on fruit trees. Interestingly, *P. syringae* can also live and spread through wind, rain, insects, and infected plants or seeds. In addition to harming plants, its ability to form ice also makes *P. syringae* also have a role of the process of cloud and snow formation in the atmosphere, making it an important part of the Earth's water cycle. Therefore, this bacterium is not only a serious threat in the world of agriculture, but also an organism with a broad ecological role in nature (Córdova et al., 2023). *Pseudomonas syringae* bacteria are ubiquitous in natural and artificial environments. *Pseudomonas syringae* has been cultivated from clouds, rain, snow, rivers, and lakes (Hanlon et al., 2023).

C. Methodology

1. Research Design

This study uses a literature review method by collecting data from various secondary sources (Ramadhani & Rezania, 2023), which means data obtained not directly by researchers but through other parties or from existing documents (Imani et al., 2024), such as national and international journals, books, and other literature (Wardhani & Harmin, 2020). The stages of the research conducted are (1) determining the main topic or variable to be discussed in the article (Arhamar, 2025), (2) identifying the research focus based on information gathering (Marera, 2022), (3) reading relevant sources related to the research focus, (4) compiling and (5) processing the reviewed research notes, and (6) producing a report in the form of a scientific article (Rahardjo, 2017).

2. Instruments

The research instrument is the researcher himself (*human instrument*), where the researcher's role includes planning, data collection, analysis, interpretation of findings, and preparation of research reports (Zuhairi & Ahmad, 2020).

3. Technique of Data Analysis

The data analysis technique in this study used the content analysis technique (Arum, 2019). Content analysis is a research method that emphasizes an in-depth study of the content of information in written or printed form (Asfar, 2019) to obtain conclusions from each source studied (Rahman, Mutia, & Nur, 2023). Research data were collected using secondary data sources (Imani *et al.*, 2024) such as books, national and international journals, and other literature related to the focus of the research (Sofiah, Suhartono, & Ratna, 2020), then compiled and summarized from the sources obtained according to the research topic (Noviponiharwani, Andi, & Baharuddin, 2023), and analyzed to obtain a deeper understanding (Ramadhani & Rezanita, 2023) regarding the uniqueness of *Pseudomonas syringae* bacteria in forming ice. After collecting data from relevant research journals, analyze and discuss the results (Zuraida, Imas, & Zipo, 2021).

D. Findings and Discussion

1. Findings

a. Occurrence and Habitat

Pseudomonas syringae is a highly adaptable bacterium, ubiquitously present in diverse environments such as soil, plant surfaces, freshwater bodies, and the atmosphere. Its presence on plant leaves and tissues is well documented, where it acts both as an epiphyte and a pathogen. Under specific environmental conditions, particularly low temperatures, *P. syringae* produces ice nucleation proteins (INPs) that catalyze the formation of ice crystals on plant surfaces. This process not only causes physical damage to plant tissues, facilitating bacterial invasion, but also contributes to the bacterium's survival and dispersal in nature¹.

Recent studies have expanded our understanding of *P. syringae*'s ecological range. It has been isolated from atmospheric sources such as clouds, rain, and snow, confirming its role in atmospheric processes and the global water cycle (Hanlon *et al.*, 2023). The bacterium's ability to induce freezing at relatively high subzero temperatures (as warm as -2°C) distinguishes it from other biological and non-biological ice nucleators, which typically require much colder conditions (Schmid *et al.*, 1997).

b. Mechanisms and Impact of Ice Nucleation

The primary mechanism by which *P. syringae* influences its environment is through the production of INPs, notably the InaZ protein. These proteins serve as nucleation sites, enabling water to freeze at higher temperatures than would otherwise be possible. Structurally, InaZ adopts a β -helical conformation that organizes interfacial water, enhancing the efficiency of ice nucleation (Roeters *et al.*, 2021). This ability has profound implications for both agriculture and atmospheric science¹.

In agriculture, the ice-nucleating activity of *P. syringae* is a double-edged sword. On one hand, it is a major cause of frost injury in crops, leading to significant economic losses due to reduced yields (Barranquero *et al.*, 2019). On the other hand, humans have exploited this property for beneficial purposes, such as the production of artificial snow for winter sports and climate research.

c. Ecological and Atmospheric Significance

Beyond its agricultural impact, *P. syringae* plays a critical role in atmospheric processes. Its presence in clouds and precipitation events supports the hypothesis that biological particles can act as efficient ice nuclei, influencing cloud formation, precipitation patterns, and even the hydrological cycle at local and global scales (De Araujo *et al.*, 2019; Hanlon *et al.*, 2023). The evolutionary history of the genus suggests that its adaptation to both terrestrial and aquatic habitats predates the development of modern agriculture, highlighting its long-standing ecological significance (Morris *et al.*, 2013).

d. Genetic Diversity and Adaptation

Genomic studies reveal that *P. syringae* possesses a wide array of genes associated with secretion systems, motility, and resistance to antibiotics and heavy metals, supporting its

survival in varied environments. The bacterium's genetic diversity is reflected in the existence of multiple pathovars, each adapted to infect different plant hosts. Notably, the strain *P. syringae* pv. *tomato* is a well-known pathogen responsible for bacterial speck in tomatoes. Recent research also points to the potential use of bacteriophages as biological control agents to mitigate the impact of *P. syringae* in agriculture.

e. Broader Scientific Implications

The study of *P. syringae* underscores the importance of microorganisms in both natural and engineered systems. Its unique ice-nucleating properties bridge the disciplines of microbiology, plant pathology, atmospheric science, and biotechnology. Understanding the molecular mechanisms and ecological roles of *P. syringae* not only advances basic scientific knowledge but also informs practical applications in agriculture, climate engineering, and disease management.

f. Future Directions

Further research is needed to elucidate the regulatory networks controlling INP expression and to explore the potential for manipulating *P. syringae* populations in agricultural and atmospheric contexts. The development of targeted biocontrol strategies, such as phage therapy, holds promise for reducing crop losses while minimizing environmental impact. Additionally, the continued exploration of microbial contributions to atmospheric processes may yield novel insights into climate regulation and the global water cycle.

2. Discussion

The findings confirm that *Pseudomonas syringae* is not only a major plant pathogen but also plays a unique ecological role as an ice-nucleating agent in the atmosphere. Its ability to produce ice nucleation proteins (INP) enables the bacterium to induce ice formation at relatively high temperatures, which can cause frost damage to crops and significant agricultural losses (Barranquero *et al.*, 2019). This mechanism also explains the bacterium's presence in various environments, from plant surfaces to clouds and precipitation, highlighting its adaptability and ecological importance (Hanlon *et al.*, 2023).

Recent studies have shown that the ice-nucleating activity of *P. syringae* not only impacts agriculture but also affects atmospheric processes, such as cloud glaciation and precipitation (De Araujo *et al.*, 2019). The discovery of this bacterium in rain, snow, and marine environments further supports its role in the global water cycle (Schmid *et al.*, 1997). This dual function, being both a threat to crops and a key player in natural weather phenomena, demonstrates the complex and significant impact of *P. syringae*.

Understanding the molecular mechanisms of ice nucleation, especially the structure and function of INP like InaZ, is essential for both agricultural management and climate science (Roeters *et al.*, 2021; Bieber & Borduas-Dedekind, 2024). Future research should focus on integrated management strategies, including the use of bacteriophages as biocontrol agents, and explore the potential application of *P. syringae* in biotechnology.

E. Conclusion

Pseudomonas syringae is a gram-negative, rod-shaped bacterium with spherical colonies that is widely distributed in various environments and plants and is known for its ice nucleation activity mediated by ice-nucleating proteins such as InaZ. Although this bacterium causes pathogenesis in a number of plant diseases, it has important ecological roles, including the formation of ice, clouds, and precipitation. Its adaptability gives it the ability to survive in a wide range of climatic conditions, and despite its high genetic variation, common strains have high ecological relevance. The use of *P. syringae* in producing artificial snow shows the potential for further application of this bacterium.

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