

A review: Bacterial Pustule of Soybean Caused by *Xanthomonas Axonopodis* Pv. *Glycines*: Epidemiology, Economic Impact, and Status in Indonesia

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Abstract

Soybeans (*Glycine max* L. Merrill) are the most important commodity after rice and corn. Soybeans are used as food, feed, and materials for the food industry. One of the major biological constraints to soybean productivity is bacterial pustule disease caused by *Xanthomonas axonopodis* pv. *glycines* (Xag), a pathogen favored by warm and humid environments. This review synthesizes current knowledge on the epidemiology, pathogenesis, and economic losses associated with soybean bacterial pustule, with particular emphasis on its status in Indonesia. Available studies indicate that bacterial pustule is widely distributed in major soybean-producing regions, with reported disease severity ranging from 12% to 70%. Under favorable environmental conditions, yield losses may reach 7–40%, primarily due to defoliation, reduced photosynthetic efficiency, and decreased seed size and number. Disease development is strongly associated with temperatures of 26–30 °C, high relative humidity, and prolonged leaf wetness, conditions commonly observed during the rainy season in tropical agroecosystems. Indonesia's warm and humid tropical climate provides suitable conditions for pathogen survival, dispersal, and infection, particularly during the rainy season. This review highlights key knowledge gaps and underscores the need for integrated epidemiological assessments to mitigate yield losses and to support sustainable soybean production in Indonesia.

Keywords: Environment; photosynthetic; soybeans

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Introduction

Soybeans (*Glycine max* L. Merrill) are the most important commodity after rice and corn. Soybeans are used as food, feed, and materials for the food industry. The demand for soybeans continues to increase year over year, as Indonesia's population grows. Indonesia's soybean production in 2023 is predicted to reach 349,100 tons, with the majority of the demand being met through imports of 2.16 million tons. This national demand is projected to continue to increase. This makes soybeans the second-most-imported food ingredient after wheat. Soybean imports are expected to increase each year as national soybean production declines [1].

One of the main problems in soybean cultivation is disease, especially bacterial pustule disease. This disease, caused by *Xanthomonas axonopodis* pv. *glycines*. This is

a serious problem that causes a 12-40% reduction in soybean seed size and number. In susceptible varieties and in environments that support the bacteria's growth, the susceptibility decreases. It also reduces productivity by up to 57.61% and decreases the size and number of soybean seeds by 12-40% [2] [3]. This disease is common in warm and humid areas [4]. In Indonesia, bacterial pustule disease in soybean plants is spread across several regions, such as West Java, Central Java, the Special Region of Yogyakarta, Lampung, South Sulawesi, and West Sumatra [5].

The initial symptoms of leaf pustules are small green spots on the palms, which may turn yellow. There can also be yellow spots with bumps in the middle that protrude on the top and bottom of the leaves. Then the symptoms develop into brown [6], [7], [8]. Pustule bacteria also cause necrosis and premature leaf fall in

soybeans. Pustules are a mechanism to respond to bacterial infections through hypertrophic changes in parenchymal tissue. Pustules are accompanied by a drastic increase in the content of indole-3-acetic acid in the host tissue [9].

Pathogen attacks greatly affect plant productivity. Each variety reacts differently to pustule bacteria, with reactions influenced by the variety's susceptibility, the strain's virulence, and environmental conditions [10]. Control of this disease can be achieved through various methods, including resistant varieties, chemical control, and biological agents. The warm, humid climate typical of Indonesia is ideal for the growth and development of soybean pustules.

Research on soybean pustule has also been widely conducted. Soybeans are not native to Indonesia, so this review aims to synthesize current knowledge on the distribution, environmental drivers, and economic importance of bacterial pustule disease, while highlighting key research gaps and the need for biotechnological approaches to support sustainable soybean production in Indonesia.

Economic loss of soybeans caused by bacterial pustule

Bacterial pustule of soybean caused by *Xag* is economically important primarily because of its direct effects on yield reduction, deterioration of seed quality, and production instability, rather than the overall economic value of soybean as a commodity. Bacterial pustule disease is seed-borne, and infected seeds can serve as a primary source of inoculum, facilitating the pathogen's spread to new areas. That can lead to considerable crop losses and reduce plant quality [11].

Studies have shown that seed infection rates can reach up to 8% [12]. These levels of seed infection can cause an epidemic if environmental conditions are right. Small amounts of seed infection can bring live bacteria into production fields, allowing the pathogen to infect cotyledons and young leaves early in plant growth. Early infection disrupts normal plant development, limits leaf growth, and increases the likelihood that the disease will spread throughout the plant. Diseases that start at this stage are important for how severe the outbreak becomes and how much crop is lost, showing why seed-borne transmission matters for the persistence of bacterial pustules.

The disease can cause losses from 7-11% [13] and, under favorable conditions such as warm temperatures and high humidity, can reduce the size and number of soybean seeds by

12-40%, as well as decrease productivity by 57.61%. [2] High disease severity can cause total defoliation, reduced photosynthetic efficiency, and decreased pod size and number in soybean plants [14]. Field studies have reported that infection rates reaching 75% may result in soybean yield losses of approximately 53% [15].

Additional evidence further illustrates the economic significance of bacterial pustule by demonstrating that disease incidence levels of 10.5% and 77.8% can result in yield losses of up to 37.7% [16]. Among these losses, approximately 50–80% have been attributed to cotyledon infection, which disrupts early plant development, while 18–30% are associated with leaf infection that reduces photosynthetic capacity and accelerates defoliation. In addition to yield quantity losses, reductions in seed size and seed number significantly affect market quality and seed viability, further increasing the economic burden of the disease. Collectively, these findings highlight the substantial economic threat posed by bacterial pustule and emphasize the importance of early detection, effective seed health management, and integrated disease control strategies to minimize yield losses in soybean production systems.

Pathogenesis

Xanthomonas axonopodis has been identified as having a wide host range, including tomatoes [17], lettuce, radish, soybean, Arabidopsis [18], and rice [19]. The pathogen grows between pH levels of 4.0 and 8.0, and pH 7.0 is the optimum for bacterial colonies to grow. This bacterium cannot grow at extreme temperatures below 10°C or above 45°C [20].

This bacterium is a Gram-negative bacterium [21], [22], [23], [24]. *Xag* has a rod-shaped, yellow pigment and a single polar flagellum [25]. This bacterium is an obligate aerobe and positive for amyolytic activity.

These bacteria initially grow as epiphytes on leaf surfaces [25] then infect the leaf through the stomata or injured parts [21]. This pathogen subsequently spreads systemically through the vascular system and then colonizes the mesophyll parenchyma [28]. *Xag* possesses several genes that enable it to utilize carbon resources in soybeans, which are regulated in the apoplast. These include genes encoding citrate complex transporters, succinate-semialdehyde dehydrogenase, and carbohydrate transport systems [29].

Xag activates protein effectors and the type III secretion system (T3SS) in host plant cells, which are crucial for the pathogen's pathogenicity and virulence [28], [30]. The virulence of this bacterium is also influenced by the production of indoleacetic acid, cytokinins, bacteriocins [31], extracellular polysaccharides [32], toxins, and proteases [31]. The *avrXg1* gene contributes to virulence by providing resistance in a gene-for-gene manner [32], while the *flgK* and *pilD* genes are required for motility and affect biofilm formation and virulence in soybeans [33]. Motility, extracellular protease activity, and biofilm formation are critical virulence factors for *Xag*. Extracellular proteases are major secondary metabolites and important virulence factors, whereas swimming motility and biofilm formation play key roles in the attachment process [34].

Epidemiology

The development of the disease is also influenced by leaf age, the duration of wet leaves, temperature, and humidity [35][36]. *Xanthomonas* spp. can grow and spread rapidly at temperatures of 25-35 °C [37]. Meanwhile, the optimal temperature range for the development of bacterial pustule disease is 26°C to 30°C [38]. *Xag* is also an epiphytic bacterium that needs high humidity to survive. These temperature ranges are commonly observed in tropical and subtropical soybean production regions, which may increase the risk of disease outbreaks. In addition, *Xag* is capable of surviving as an epiphytic bacterium on leaf surfaces, where high humidity and prolonged leaf wetness provide favorable conditions for bacterial colonization, multiplication, and subsequent infection processes [25], [39]. Leaf age also influences disease susceptibility, as younger leaves often provide more suitable physiological conditions for bacterial establishment and symptom development.

Xag is an airborne pathogen that is transmitted via air and water droplets [6]. This disease is also influenced by the season, as the bacteria spread through water or windblown rain [40]. Irrigation practices and canopy density may further contribute to prolonged leaf wetness, enhancing infection efficiency and accelerating disease progression. Furthermore, fluctuations in minimum and maximum temperatures have been shown to affect pathogen survival, bacterial multiplication rates, and disease severity, indicating that microclimate variability plays a critical role in bacterial pustule epidemiology [41].

Variability in environmental conditions among soybean production areas may contribute to differences in disease incidence and severity across regions. Interactions between environmental factors and host susceptibility may influence the temporal and spatial dynamics of disease outbreaks. Understanding these epidemiological drivers is essential for developing disease prediction models, improving surveillance strategies, and designing environmentally adapted disease management approaches. However, integrated epidemiological studies examining the combined effects of climate variability, host resistance, and pathogen population dynamics remain limited, particularly in tropical soybean production systems.

Bacterial pustule in Indonesia

Soybeans are plants that originate from subtropical areas, but are also widely cultivated in tropical countries such as Indonesia. These different climate conditions not only affect the growth and yield of soybeans, but also affect the presence of pathogens that attack them. One of the diseases that is often found is bacterial pustule. Bacterial pustule is a common disease in Indonesia.

Bacterial pustule has been reported in several soybean-producing provinces in Indonesia, including East Java, West Java, Central Java, West Sumatra, and Southeast Sulawesi, where disease severity has been reported to range from 12-70% [12], [42], [43], [44], [45], [46]. The severity of the disease found in Indonesia is higher than found in Benin, West Africa, according to research by [8], the range of severity of bacterial pustule was 5.95 to 26.14%. Meanwhile, in Korea, with a subtropical climate, the severity of the disease is almost the same as in Indonesia. The national severity of pustule disease in Korea during 2015-2017 was 27%, and several provinces had a severity of more than 50% [47].

The pathogen could cause a disease severity of 28.33% at 22.4°C and 30.4°C with humidity ranging from 36% to 68%. However, no disease was observed at temperatures between 26°C and 37°C with humidity levels ranging from 21% to 61% [48]. During the dry season, the incidence of pustule disease was low due to lower humidity and the absence of rainfall, which limits the pathogen's growth and spread. The disease response could be attributed to either soybean varieties' susceptibility to bacterial pustule or to the increased aggressiveness of the bacterial strain under specific environmental conditions, which

promote disease development [46], [48]. The severity of the disease was higher during the rainy season in both intercropping and monoculture systems. The selection of monoculture and intercropping planting systems affects the severity of bacterial pustule disease in soybean plants. Monoculture planting results in a higher average severity compared to intercropping [6].

Disease control

Research related to controlling this disease has also been widely conducted. Control methods include regulating the planting system and using organic or biological materials. Intercropping can reduce the severity of pustule disease. Disease control can also use biological agents, such as plant growth-promoting rhizobacteria (PGPR) and local microbial consortia. Endophytic bacteria isolated from soybean roots also can inhibit pustule development and enhance plant growth [49].

The intensity of bacterial pustules in plants induced with endophytic bacterial isolate formulas ranged from 11.23% to 26.77%, compared to 35.58% in the control group. The highest intensity of soybean leaf pustule disease occurred in the control plot without bacterial formulations, at 16.63%. In plots treated with bacterial formulations, pathogen infection was lower, with infection rates ranging from 3.65% to 5.14% [50], [51]. *Pseudomonas fluorescens* SP007s have been reported to significantly reduce disease severity and pathogen population on leaves by priming plant defense responses and increasing salicylic acid accumulation [52].

Bacillus bacteria can also be used to control pustule disease. Without control, the disease severity reached 70.51%. In plants treated with *Bacillus*, the disease severity ranged from 10% to 19.58% [7]. Besides directly controlling pustule disease, several phyllosphere bacteria can significantly increase plant height, branch number, and leaf number in soybean plants [2]. The Btt formula (*Bacillus thuringiensis* pv. *Toumanoffi*) suppressed the incidence and severity of Xag compared to the control [53].

Antagonistic microbes can be used as biological agents to control bacterial pustules, either singly or in consortia. Single antagonistic microbes can inhibit the growth of *Xag*. The antagonistic microbial consortium of *Bacillus subtilis*, *Pseudomonas fluorescens*, and *Trichoderma* spp. has an effect equivalent to the bactericide Streptomycin sulfate in suppressing the development of bacterial pustule disease in

soybeans [54]. *In vitro*, the antagonistic bacteria *Corynebacterium* sp. and *Bacillus* sp. can suppress the growth of *Xag* with a level of suppression comparable to that of a bactericide [5].

Conclusion

Bacterial pustule caused by *Xanthomonas axonopodis* pv. *Glycine* is an important foliar disease that affects soybean productivity under favorable environmental conditions. Disease development is influenced by interactions among pathogen virulence, host susceptibility, and environmental factors such as temperature, humidity, and cropping practices. Evidence indicates that bacterial pustule can cause considerable disease severity and yield losses, highlighting its economic significance. In Indonesia, the disease has been reported in several soybean-producing regions where tropical agroecosystems support pathogen survival and dissemination. However, comprehensive epidemiological data, quantitative yield-loss assessments, and information on pathogen population diversity remain limited. Future research should focus on integrated disease surveillance, molecular characterization of pathogen populations, and evaluation of host resistance under diverse environmental conditions. Strengthening research that integrates biodiversity and biotechnological approaches will be essential for improving disease management and supporting sustainable soybean production in Indonesia.

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