

Stochastic modeling of *Pseudomonas syringae* growth in the phyllosphere

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ABSTRACT

Pseudomonas syringae is a gram-negative bacterium which lives on leaf surfaces. Its growth has been described using epifluorescence microscopy and image analysis; it was found to be growing in aggregates of a wide range of sizes. We develop a stochastic model to describe aggregate distribution and determine the mechanisms generating experimental observations. We found that a logistic birth–death model with migration (time-homogeneous Markov process) provides the best description of the observed data. We discuss how to analyze the joint distribution of the numbers of aggregates of different sizes at a given time and explore how to account for new aggregates being created, that is, the joint distribution of the family size statistics conditional on the total number of aggregates. We compute the first two moments. Through simulations we examine how the model's parameters affect the aggregate size distribution and successfully explain the quantitative experimental data available. Aggregation formation is thought to be the first step towards pathogenic behavior of this bacterium; understanding aggregate size distribution would prove useful to understand the switch from epiphytic to pathogenic behavior.

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1. Introduction

Epifluorescence microscopy and image analysis techniques at the single cell level offer the possibility to determine directly very specific quantitative information of bacterial behavior on leaves. The aggregation distribution of the plant-pathogenic bacterium *Pseudomonas syringae* pv. *syringae* strain B728a on leaf surfaces of greenhouse-grown bean plants has been reported using such techniques [7,31]. These bacterial cells were found to be aggregated in a great variety of sizes. In this work we develop a mathematical model to describe and explain the observed aggregation distribution.

There are several reasons to study the biological and ecological significance of aggregate formation by these epiphytic bacteria: the aggregated bacteria show increased fitness under environmental stress [31,33,41] and aggregates promote a switch of an epiphytic lifestyle on the plant's healthy leaves towards an invasive, highly pathogenic [7,40]. Thus, understanding the dynamics of aggregation and growth will facilitate the development of treatment strategies.

The aim of this work is to use a mathematical model to help understanding the mechanisms that give rise to the growth (an increase in number of viable cells through multiplication) pattern of this bacterium on leaf surfaces following inoculation with *P. syringae* pv. *syringae* strain B728a as reported in Dulla and Lindow [7]. Therein, these bacterial cells were found to be distributed in aggregates of a wide range of sizes, from single cells to aggregates with over 10^4 cells. The majority of aggregates observed were small (less than 100 cells) and aggregate sizes exhibited a strong right-hand-skewed frequency distribution. Large aggregates were not frequent on a given leaf but they contain the majority of cells present.

Rather than fitting a distribution to the experimental data, we opted for a dynamical approach which can provide information on the causes of the observed aggregation distribution and the mechanisms that generate it. Successfully describing the mechanism that cause most of the cells to be in large aggregates is of great relevance as it has important biological repercussions. Large aggregates may be protected from bactericides. A colonization pattern where the majority of the cells are located in a few large aggregates can significantly limit microbial control [31].

Our model not only gives a qualitatively correct description of the behavior of *P. syringae* growth on plant leaves but is also able to propose two mechanisms which can explain the experimental results: migration and heterogeneity of the nutrients availability. The model results agree with the aggregate size distribution

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observed by Dulla and Lindow [7], furthermore, since the model allows to investigate diverse scenarios, it is also able to describe and reproduce similar quantitative data from similar experiments from Dulla and Lindow [31].

This manuscript is organized as follows, in Section 2 we give a biological background, in Section 3 we develop the model, in Section 4 we discuss the model's simulation results and compare them to the experimental evidence available, finally in Section 5 we present general conclusions.

2. Biological background

2.1. *Pseudomonas syringae*

Although leaf surfaces constitute a hostile environment (fluctuating temperatures, relative humidity, moisture, and UV irradiation), they are often colonized by a variety of microbes. *P. syringae* is a gram-negative bacterium which is able to grow on plant leaves (the phyllosphere). This bacterium was first isolated as a pathogen of lilac (*Syringa vulgaris*), it has been studied since the early 1900s due to its pathogenic effect on crop plants [1,10,14,15,24]. *P. syringae* is also able to produce frost injury due to its ice nucleation properties [10]. On moist leaves, wild-type cells can move on surfaces from a single inoculation point, presumably by flagellum-mediated swimming and swarming [8]. Sugars such as glucose, fructose, and sucrose are the main carbon sources.

Fig. 1 This bacterium is often found in tomato, bean, olive, and tobacco among others where they can live symptomless for prolonged periods. Slight changes in the environment which favor the bacteria may cause a rapid outbreak, creating diseases (see Fig. 2) that can destroy entire crops.

2.2. Variability of the leaf surface environment

There exist several examples of heterogeneity in microbial behavior on leaves: from population distribution to communication patterns [2]. Several studies have given evidence of the heterogeneity of the leaf surface environment, both among leaves and within a leaf [30,31]. Leveau and Lindow [21] showed a highly heterogeneous availability of fructose to individual cells as they colonize the phyllosphere. McGrath and Andrews [29] give further confirmation of differences in carrying capacity among leaves and show how aggregates form around regions where there may be more nutrients available. Woody et al. [47] reports on how differences in habitat quality are primarily responsible for the variation in (*A. pullulans*) density among leaves in nature. In [34], the spatial heterogeneity of cell sizes observed on leaves suggests that

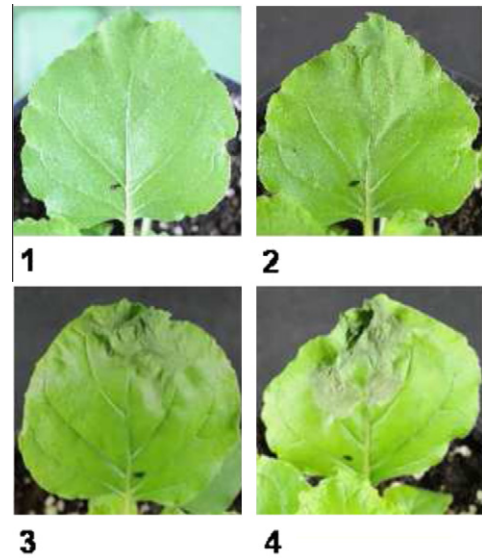


Fig. 2. Bacterial lesions caused by *Pseudomonas syringae* pv. *syringae* B728a in *N. benthamiana*, picture provided by Dr. Corina Vlot's group (Inducible resistance signalling), Institute of Biochemical Plant Pathology, Helmholtz Zentrum München. Pictures display the damage to the leaf in a period of 4 days. Reproduced with permission.

nutrient availability is quite variable on the leaf surface environment.

Other studies [46] investigated the cause of variations in fungal population density among leaves. Their experiments showed that natural populations vary greatly in density due to sustained differences in carrying capacities among leaves and suggest that the maintenance of populations close to carrying capacities indicates strong density-dependent processes.

Given this evidence, studies on the nutrients status on plants could be potentially used to manipulate microbial populations.

2.3. Relevant previous work

Formation of aggregates is a diverse and widespread phenomenon. Several examples have been investigated using mathematical modeling [9,37,44], including bacterial behavior such as colony formation [17] and bacterial communication [6].

Here we briefly review some works of relevance to our problem. Bailey [3] was among the first to use stochastic models to study collections of populations which are distributed spatially, and which are subject to birth, death, and migration to or from

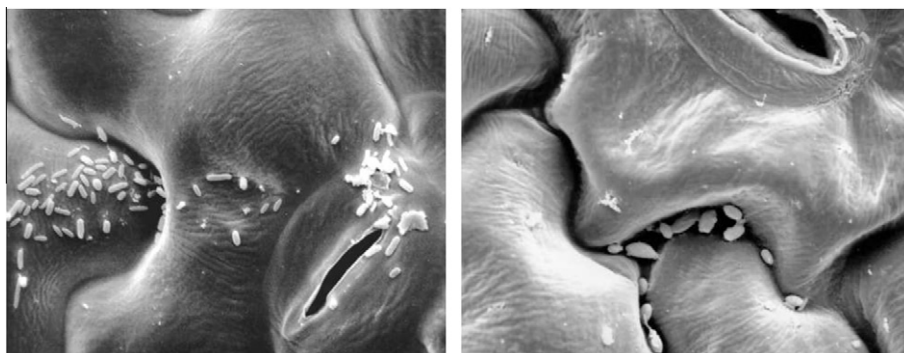


Fig. 1. Scanning electron micrographs of *Pseudomonas syringae* on bean leaves (left picture) and between epidermal cells (right picture). The opening in the lower right-hand corner of the picture on the left is a plant stomate. *P. syringae* often uses these openings to invade the plant. Pictures contributed by Prof. Gwyn Beattie, Department of Plant Pathology, Iowa State University. Reproduced with permission.

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