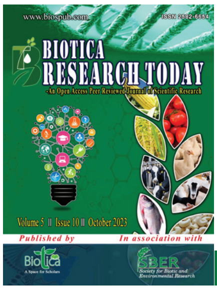

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The Phenomenon of Cheating in Plant Pathogens

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Abstract

Plant pathogens, which exist as populations going through evolutionary processes within their host, are an essential part of the soil and host microbiome. Numerous facets of virulence depend on social interactions between and within microbial populations, which are primarily mediated by multiple forms of public goods, comprising effector molecules, exo-enzymes, and quorum-sensing signalling molecules. Disease progression and virulence have social implications that significantly impact the fitness of microbes and hosts. Numerous opportunities for pathogens to deceive the host are highlighted by the molecular basis of infection events and the sequential stages of plant-pathogen interactions. Additionally, there is evidence of variation in the level of virulence exhibited by different phytopathogens. Understanding of interactions within microbes, avenues of opportunities and cheating exhibited by these microbes will enable us to get clear insight of their role in disease progression and further adoption of tactics to manage plant pathogens.

Keywords: Cheating, Opportunities, Plant pathogens, Public goods

Introduction

Populations and communities of microbes present in the soil stratum communicate with their shared host and each other and these social interactions among these groups create a variety of chances for both cooperation and conflict. The plant host may be regarded as a public good (*i.e.*, freely available for use) and its exploitation by these pathogens could lead to a tragedy of the commons, in which the virulence yields short-term gains at the expense of long-term prosperity. Thus, understanding the interactions between pathogens that are cooperative or antagonistic may worsen plant outcomes or reduce pathogen virulence. Henceforth, comprehending the basic concepts and mechanisms underlying microbial social interactions has significant implications for the way we can understand and manage the plant diseases (Friesen, 2020).

In the perspective of microbial cooperation, public goods are those compounds that benefit a group of individuals together, usually by releasing signal molecules into the extracellular environment. Numerous forms of microbial public goods exist in nature such as, extracellular enzymes, siderophores, antibiotics, exopolysaccharides (EPS), toxins and quorum sensing molecules (Smith and Schuster, 2019). They range from complex proteins to simpler metabolites and they can diffuse passively from the producing cell or be actively secreted. Extracellular enzymes, for instance, break down complex polymers into smaller particles that individual cells can absorb. Antibiotics may destroy the nearby bacteria, toxins alter host cell membrane to let nutrients out, and in environments where iron is scarce, siderophores scavenge it.

Phenomenon of Cheating

Since public goods are easily shared in microbial populations, cheaters are capable of taking advantage of them. Cheaters are a subsection of the general population who refrain from taking part in cooperative efforts but who nevertheless profit from the goods produced by cooperators without bearing any of the costs that come with them. Simple microbe culturing experiments using fluorescent tags or antibiotic-resistant

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strains can be used to demonstrate microbe cheating. Strains that produce public goods and those that don't are cultivated separately or in combination in growth media that support the production of public goods. Producers of these strains grow more quickly than non-producers when they are cultivated in separate cultures. Conversely, non-producers outgrow producers in a well-mixed coculture, and as a result, they are said to have higher "relative fitness," which is usually calculated as the ratio of the two strains' average growth rates. Furthermore, comparable experiment designs have identified density dependence and frequency dependence as fundamental characteristics of cheating on public goods. In simple terms, this suggests that in crowded communities and when there are fewer cheaters around; those who cheat can more effectively exploit those who cooperate.

Plant pathogens require social interactions with their hosts or microbes that result in the production of a public good in order for them to cheat. These public goods are represented in table 1.

Table 1: Produced public goods by various pathogens (Friesen, 2020)

Sl. No.	Disease symptom	Public good	Pathogens associated
1.	Lesions	Toxins	*Helminthosporium victoriae*
2.	Wilt	EPS	*Ralstonia solanacearum*
3.	Powdery growth	Fruiting body	Spore production and distribution
4.	Rot	Cell wall degrading enzymes	Pectobacterium carotovorum
5.	Water-soaking	EPS, HopM1 effectors	*Pseudomonas syringae, X. malvacearum*
6.	Spots (HR)	Effectors	The majority of bacteria
		Quorum-sensing signals	The majority of bacteria
		Siderophore	The majority of bacteria
7.	Gall	Habitat, Opines	*Agrobacterium tumefaciens*

Initially, the primary mode of interaction between potential pathogens and hosts is the interchange of molecules that transmit signals. Plants are known to secret diverse array of nutrients, volatiles, and diffusible small molecules into their phyllosphere and rhizosphere, giving the pathogens a chance to proliferate. Numerous bacteria secrete a wide range of small molecules, including AHLs (N-acyl-homoserine lactones), oligopeptides and cyclic dipeptides) and express a range of virulence genes exclusively in response to specific molecules' concentrations exceeding a predetermined threshold (quorum sensing) (Azimi *et al*., 2020; Rumbaugh *et al*., 2009). Particularly, the rhizosphere is the subject of extensive research and also acts as hot spots because "roots act as the guts of a plant", playing vital roles in the assimilation of nutrients. These hot spots represent sites of intense rivalry and provide opportunities for cooperation and cheating (Friesen, 2020). Considering an example wherein, a metal, Several micronutrients, in particular iron, are frequently limiting for microbial growth, and many bacteria (*Pseudomonas* spp.) can produce a variety of siderophores that improve the solubility of iron. Usually, these siderophores need a cognate receptor to be perceived by the cells of other bacteria. It is known that the pathogen *P. aeruginosa* constitutively produces multiple forms of the siderophore pyoverdine at low levels (Friesen, 2020). The upregulation of this specific type of pyoverdine siderophore occurs when one of these molecules returns to the cell complexed with iron. Pathogen infections in humans and soil frequently result in the recovery of non-pyoverdine-producing strains, which are essentially cheaters who profit from the pyoverdine produced by co-occurring cooperators (Kramer *et al*., 2019). Another typical example includes, bacteria producing biofilms, a type of extracellular matrix that forms a complex bond between cells of carbohydrates, proteins and DNA, in addition to promoting binding to plant surfaces (Friesen, 2020). It is well known that biofilms shield cells from dehydration, bacteriophage infection, predators, and antibiotics. Therefore, the secretion of biofilm matrix compounds is a public good, and nonproducing mutants may benefit from producers' mistakes. The highly reproducible experimental evolution of biofilm cheaters in cultures of *P. fluorescens* serves as best illustration. Biofilms are commonly composed of EPSs and cellulose, and a variety of bacteria have been reported to form mixed-species biofilms in both culture and in in vivo conditions. Additionally, a biofilm limits the diffusion of molecules secreted, so in this environment, bacteria that secrete enzymes that break down cell walls can be relatively certain that their behavior will be strictly localized. Even so, the production of these enzymes is expensive they provide access to everyone in the vicinity.

Conclusion

Microbes regularly communicate with their plant host or with one another, which produces free public good during the interaction there is every possibility of emergence of cheater strains by exploiting the resources produced by their co-partners and there are numerous studies highlighting the role of these cheater strains in controlling the virulent strains. Our main strategy in controlling plant diseases must be focused on these cheater strains and studying their behaviour *in-planta* or *in-vitro* conditions.

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