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## Review: Fruit collapse and heart rot disease in pineapple: Pathogen characterization, ultrastructure infections of plant and cell mechanism resistance

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**Abstract.** Cano-Reinoso DM, Soesanto L, Kharisun, Wibowo C. 2021. Review: Fruit collapse and heart rot disease: Pathogen characterization, ultrastructure infections of plant and cell mechanism resistance. *Biodiversitas* 22: 2477-2488. Fruit collapse and bacterial heart rot are diseases in pineapple caused by *Erwinia chrysanthemi* (later classified as *Dickeya zaeae*) which are increasingly prevalent in the last decade, causing devastating production loss in pineapple cultivation. Yet, comprehensive knowledge to tackle such diseases is limited, understandably due to the relatively new emerge of the diseases. Here, we review the causes of bacterial heart rot and fruit collapse, stages of infection, typical symptoms and the occurrence of resistance mechanisms in plants. In pineapple, the fruit collapse is noticeable by the 6 ease of juice and gas bubbles, also the shell of the fruit that turns into olive-green. Meanwhile, bacterial heart rot is characterized by water-soaked zones on the leaves, the formation of brown streaks on the lamina and in the mesophyll, and light-brown exudate in the blisters. The most common means of penetration into the host plant used by this type of pathogen is through plant natural openings, injuries and wounds, and entire surfaces. Concurrently, plants and fruits develop disease-resistant mechanisms to inhibit infection growth under this pathogenic attack. These mechanisms can be divided into hypersensitive reactions, locally acquired resistance, and systematic acquired resistance. In addition, pathological infections produce an interaction of the cell wall with pectolytic enzymes. Understanding the membrane breakdown process carried out by these enzymes has become critical to a pineapple protection plan. This review suggests that future research to tackle fruit collapse and bacterial heart rot can be focused on disease-resistant mechanisms, and their effects on the cell wall status with an enzymatic characterization.

**Keywords:** Cell wall, *Dickeya*, *Erwinia chrysanthemi*, low-acid, pectate lyase

### INTRODUCTION

<sup>2</sup> Pineapple (*Ananas comosus* L. Merr.) is an important crop in many tropical areas of Latin America, Asia, and Africa. Among various cultivars of pineapple consumed globally, the low-acid hybrids have increased their popularity in the fresh market, and therefore the cultivations grew in the last years. However, these hybrids present emerging challenges in the cultivation and post-harvest handling activities for the breeders and shippers (Chen et al. 2009; Zuraida et al. 2011; Žemlička et al. 2013; Kleemann 2016).

A fundamental problem with these hybrids is the increased susceptibility to natural flowering and abrasion injury (Chen et al. 2009; Zuraida et al. 2011; Žemlička et al. 2013). Moreover, after harvest, the fruit can produce excessively low acidity due to an undesirable increase in sugar content, which leads to physiological abnormalities (Chen et al. 2009; Žemlička et al. 2013; Soteriou et al. 2014; Gu et al. 2016; Ibrahim et al. 2016). In addition, due to their physicochemical properties, they are prone to various diseases (Žemlička et al. 2013; Soteriou et al. 2014).

Fruit collapse and bacterial heart rot are common diseases in pineapples' low-acid hybrids. In countries such as Malaysia, Brazil, and Indonesia, fruit collapse has recently been recorded (Rohrbach and Johnson 2003; Korres et al. 2010; Prasetyo and Aeny 2014). Fruit collapse, a disease that has never been identified before 2014 in Indonesia, causes the fruits got rotten and collapsing immediately three to two weeks close to fully ripening, resulting in considerable losses by 50% suffered by the plantation (Peckam et al. 2010; Prasetyo and Aeny 2014; Sueno et al. 2014). Meanwhile, bacterial heart rot cases have been documented in Malaysia, Costa Rica, Brazil, Philippines, and Hawaii (Rohrbach and Johnson 2003; Kaneshiro et al. 2008; Ramachandran et al. 2015; Pires de Matos 2017).

While the two diseases are increasingly prevalent in pineapple cultivation in tropical regions, comprehensive knowledge to tackle such diseases is limited, understandably due to the relatively new emergence, especially the fruit collapse disease. As such, the understanding of the factors that make the pineapple plant and fruit more exposed to these diseases' infection is urgently required, in particular studies on the mechanism of

interaction between the host and the environment, including the physicochemical process involved, primarily in low acid hybrids, which are more susceptible to these infections.

In general, the aim of this article is to review the causes of bacterial heart rot and fruit collapse, stages of infection, typical symptoms and the occurrence of resistance mechanisms in plants. The discussion of the mechanisms of resistance in plants is broadly described in order to aid a better understanding of the development of the symptoms of these diseases. We expect that the comprehensive issues discussed in this review can provide guidance, not only for scientific purposes (e.g., current knowledge gap, direction for future research), but also for management practices of low-acid pineapple hybrids since nowadays these varieties are the most predominant in the fresh market.

### FRUIT COLLAPSE AND BACTERIAL HEART ROT: DEFINITION AND CHARACTERISTICS

Fruit collapse is a disease in pineapple caused by *Erwinia chrysanthemi* bacteria that was later classified as *Dickeya zae* (Aeny et al. 2020). This disease probably originates from Malaysia (Rohrbach and Johnson 2003; Pires de Matos 2017; Aeny et al. 2020); becomes economically important due to its distribution in pineapple plantations, especially in Southeast Asian countries where the production of low acidic hybrids for fresh fruit has increased (Rohrbach and Johnson 2003; Pires de Matos 2017; Prasetyo and Aeny 2014; Aeny et al. 2020).

Ants, beetles and flies are vectors of these diseases, transporting their pathogen to flowers from other collapsed fruit and plants with bacterial heart rot infections (Rohrbach and Johnson 2003; Pires de Matos 2017; Pires de Matos 2019; Oculi et al. 2020). The insects are attracted to the nectar of the plant, which is exposed during the open flower stage. Therefore, during this stage, the site of infection is created where the pathogen enters the developing fruit. This pathogen remains latent in the ovary, however its activity increase between two to three weeks before ripening, when sugar levels increase rapidly and enzyme levels like polyphenol oxidase (PPO) decline, (Rohrbach and Johnson 2003; Pires de Matos 2017; Pires de Matos 2019; Boluk et al. 2020; Boluk et al. 2021).

Infected fruits are characterized by the release of an exudation of juice and gas that create bubbles (Rohrbach and Johnson 2003; Pires de Matos 2017; Aeny et al. 2020). Due to the high carbohydrates content in the fruit flesh, *Dickeya zae* bacteria, subject to its anaerobic characteristic, use this media to ferment sugars to lactic acid and establish its growing pattern (Gänzle 2015; König and Fröhlich 2017; Paull and Chen 2018; Tenea et al. 2020). The color of the fruit shell turns olive-green, and the internal part of the fruits show cavities within the flesh's skeletal fibers (Figure 1) (Rohrbach and Johnson 2003; Pires de Matos 2017; Aeny et al. 2020).

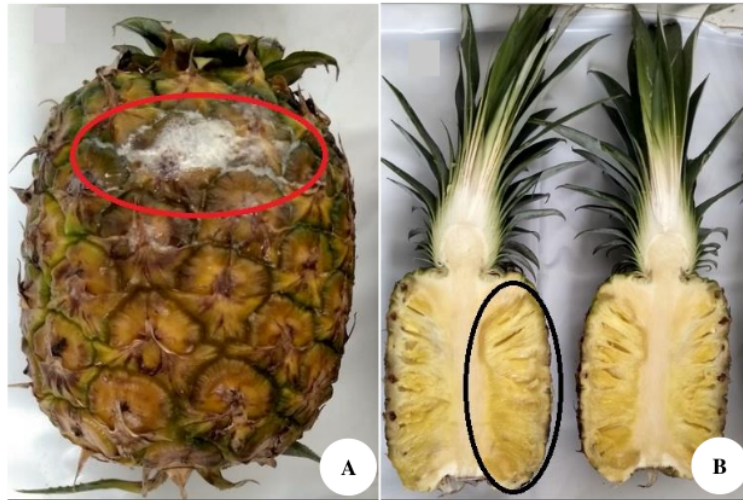
On top of that, pineapple bacterial heart rot is another disease caused by *Erwinia chrysanthemi* (*Dickeya zae*),

which is characterized by water-soaked symptoms on the white basal side of the leaves located in the central whorl (Rohrbach and Johnson 2003; Shen et al. 2013; Pires de Matos 2017; Aeny et al. 2018; Sipes and Pires de Matos 2018). The infection can spread to the whole leaf basal portion. The spread can also occur on the leaves' green mid-portion, causing an olive-green color with a bloated appearance. When the infection of the green portion of the leaf is captured, a dark border is created (Figure 2) (Rohrbach and Johnson 2003; Pires de Matos 2017; Ratti et al. 2018; Sipes and Pires de Matos 2018). The symptoms of fungal heart rots can be distinguished from those of bacterial heart rot, as no extension of the infection is observed in the green areas of older leaves (Rohrbach and Johnson 2003; Martin and Rahmat, 2017; Pires de Matos 2017; Aeny et al. 2018; Ratti et al. 2018; Sipes and Pires de Matos 2018).

According to Kaneshiro et al. (2008), in their description of *E. chrysanthemi* from a pineapple bacterial heart rot outbreak that occurred in Hawaii in 2003, symptoms of this disease usually began with water-soaked areas in the leaves around the apical meristem, followed by the creation of brown streaks over the lamina and mesophyll tissues. They affirmed that frequently characterized by gas, these lesions are representative of the disease and that eventually, a brown-light exudate can emerge from the blisters when the leaves begin to rot.

Like in fruit collapse disease, the primary inoculum source of bacterial heart rot is considered to be exuded juice of previously infected plants. On the contrary, the infested seed material like suckers, slip, or crown does not represent an essential source of infection because the bacteria do not survive long on leaf surfaces (Rohrbach and Johnson 2003; Davidsson et al. 2013; Pires de Matos 2017; Sipes and Pires de Matos 2018). According to Rohrbach and Johnson (2003), and Sipes and Pires de Matos (2018), the infection occurs through the stomata, and the bacteria can be transmitted primarily by insects, like the big-headed ants (*Pheidole megacephala*) or the Argentine ant (*Linepithema humile*); also, by wind and windblown rain. After a meristem infection, the apical and lateral buds, heart and stem of the pineapple can easily detach from the subterranean part of the plant within a few days (Kaneshiro et al. 2008; Nykyri et al. 2012; Sipes and Pires de Matos 2018).

Plants that are four to eight months old are more likely to have this infection. Common pineapple plant cultivations are also thought to be more susceptible than the ratooning (Rohrbach and Johnson 2003; Kaneshiro et al. 2008; Pires de Matos 2017; Sipes and Pires de Matos 2018). The susceptibility appears to be linked to the growth of plants because a low leaf water status has been reported to limit infection rate (Rohrbach and Johnson 2003; Kaneshiro et al. 2008; Pires de Matos 2017; Sipes and Pires de Matos 2018). Under optimal environmental conditions for the development of this disease, its entire cycle occurs between one and two weeks (Rohrbach and Johnson 2003; Sipes and Pires de Matos 2018).



**Figure 1.** The symptoms of fruit collapse disease in pineapple after harvest. A. Release of gas by bubbles together with olive-green color in the shell (red circle). B. Cavities within the skeletal collapsed fibres in the flesh (black circle).



**Figure 2.** The symptoms of bacteria heart rot disease in the pineapple plant. In both parts of the photo, a water-soaked lesion is exhibited on the leaves' white basal portion, located in the central whorl. The green mid-portion of the leaves shows the olive-green color and dark border formed. A. Aerial view of the plant peduncle (red circle). B. Internal view after removing the peduncle (yellow circle).

#### PATHOGEN HISTORY, IDENTIFICATION AND NEW GENUS CLASSIFICATION

*Erwinia chrysanthemi* is a pathogen that occurs in many host plants in the tropics and subtropics region (Rohrbach and Johnson 2003; Sipes and Pires de Matos 2018). This bacteria can potentially thrive at higher temperatures than other soft rot bacteria. The virulence of this pathogen is linked to the ability to produce large amounts of

*endopolygalacturonic transeliminase* (Rohrbach and Johnson 2003; Sipes and Pires de Matos 2018).

Bacterial heart rot and fruit collapse of pineapple were first recorded in 1927 and 1935, respectively, by Thompson in 1937, but the pathogen involved was not isolated until Johnston was working on it in 1957 and discovered that a bacterium was responsible for the diseases. According to Johnston investigations on the morphology, physiology and pathogenicity, it was concluded that it was a strain of



*Erwinia carotovora* subsp. *carotovora* which was distinct from those affecting vegetables (Lim 1974; Kaneshiro et al. 2008; Peckam et al. 2010; Marrero et al. 2013; Green and Nelson 2015; Leblanc et al. 2016; Kanda and Minshull, 2020).

Interest in both diseases increased, and initial taxonomical work showed that the organism differed in specific physiological characteristics from *E. carotovora* subsp. *carotovora* (Lim 1974; Kaneshiro et al. 2008; Peckam et al. 2010; Marrero et al. 2013; Green and Nelson 2015; Kumar et al. 2017; Hu et al. 2018). With the help of Commonwealth Mycological Institute, the organism was finally identified as *Erw. chrysanthemi* Burkholder et al. (Lim 1974; Kaneshiro et al. 2008; Peckam et al. 2010; Marrero et al. 2013; Green and Nelson 2015; Li et al. 2020). Furthermore, *E. chrysanthemi* was first described as a pathogen of *chrysanthemum* in North America, later on, philodendron, and Syngonium (Whelburg 1970; Kaneshiro et al. 2008; Bertani et al. 2013; Marrero et al. 2013; Green and Nelson 2015). Like pineapple fruit collapse and bacterial heart rot, symptoms were also detected in those plants consisted of initial necrosis, followed by a collapse of the tissue (Lim 1974; Kaneshiro et al. 2008; Peckam et al. 2010; Czajkowski et al. 2011; Marrero et al. 2013; Green and Nelson 2015; Krzyzanowska et al. 2019).

Both *E. chrysanthemi* and *E. carotovora* are facultative anaerobic bacteria that survive in the soil and cause water-soaking and rot symptoms in pineapple heart and leaves (Rohrbach and Johnson 2003; Kaneshiro et al. 2008; Peckam et al. 2010; Liao et al. 2014; Zhou et al. 2015; Sipes and Pires de Matos 2023). However, *E. carotovora* only produces localized rot when plants are wounded or grown under stress conditions, while *E. chrysanthemi* can generate a systemic rot that moves from leaves to heart (or vice versa) ignoring any stress factor displayed. In addition, *E. carotovora* subsp. *carotovora* infections develop immediately, meanwhile, *E. chrysanthemi* can cause latent infections in planting stocks that can lead to severe epidemics in places not previously affected by the disease (Kaneshiro et al. 2008; Peckam et al. 2010; Adeolu et al. 2016; Prokić et al. 2020). Therefore, differentiation of *E. chrysanthemi* from *E. carotovora* subsp. *carotovora* is essential for appropriate regulation of imported planting materials, especially in areas where the disease has not been previously detected (Kaneshiro et al. 2008; Peckam et al. 2010; Martinez-Cisneros et al. 2014; Wang et al. 2020).

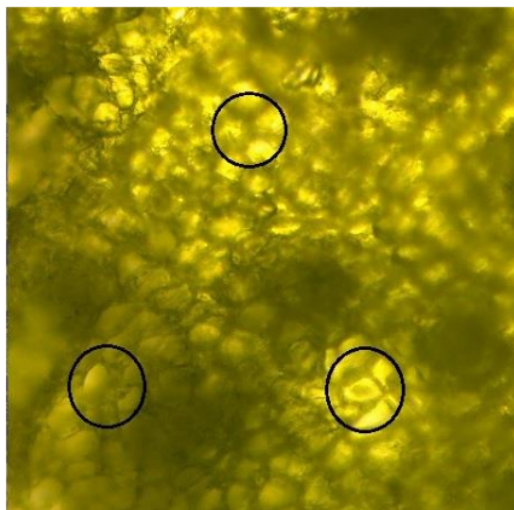
*Erwinia chrysanthemi* and *E. carotovora* subsp. *carotovora* were later reclassified to the genus *Pectobacterium* as *Pectobacterium chrysanthemi* and *P. carotovorum* subsp. *carotovorum*, respectively. Furthermore, a significant taxonomic change was later proposed in which *E. chrysanthemi* was divided into six species under the new genus *Dickeya*, *Dickeya chrysanthemi*, *D. paradisiaca*, *D. dadantii*, *D. dianthicola*, *D. dieffenbachiae*, and *D. zea* (Kaneshiro et al. 2008; Peckam et al. 2010; Parkinson et al. 2014; Sueno et al. 2014; Zhang et al. 2014; Tian et al. 2016); during that change, two strains of *E. chrysanthemi* isolated from pineapple plants were renamed as *Dickeya zea* and *Dickeya* sp. Also, in the species characterization for *D. dadantii*, the pineapple was listed as a typical host plant

(Kaneshiro et al. 2008; Peckam et al. 2010; Sueno et al. 2014). In concomitance with this, Aeny et al. (2020) also named *D. zea* as the strain established on pineapple variety for a characterization and host range assessment of fruit collapse and heart rot disease in Lampung, Indonesia.

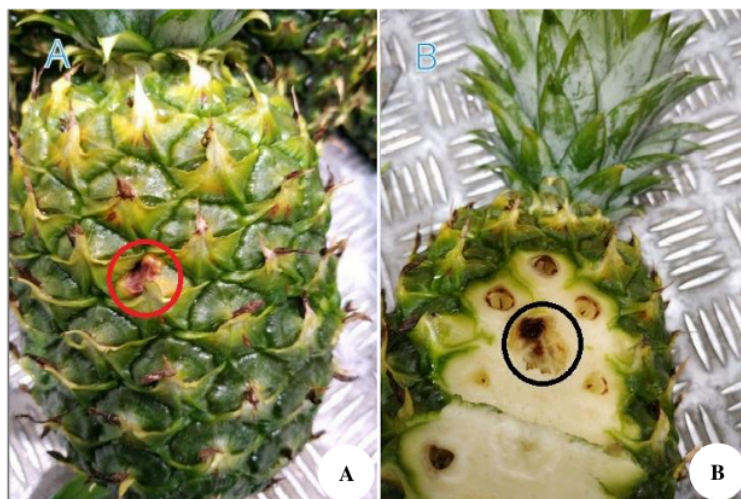
In addition, Brady et al. (2012) reclassified this genus with the help of phylogenetic analyzes, eliminated *D. dieffenbachiae*, and divided *D. dadantii* into two subspecies, *dieffenbachiae*, and *dadantii*. Recently, the addition of a new species, *D. solani*, has been proposed to encompass biovar 3 strains of the predominant blackleg and slow wilt pathogen of potato in Europe (Toth et al. 2011; Van der Wolf 2013; Czajkowski et al. 2014; Suharjo et al. 2014; Sueno et al. 2014).

### PATHOGEN PENETRATION THROUGH PLANT ULTRASTRUCTURE

Successful infection of the plant and fruit by this pathogen involves its movement towards the plant surface, following penetration and its proliferation inside the host tissues immediately after entry (Huang 1986; Melotto et al. 2008; Yadeta and Thomma 2013; Kim 2019; Campilho et al. 2020). After interactions with the cuticle, the most common ways of penetration into the host plant and fruit used by this pathogen can be classified as: penetration through plant natural openings (stomata, hydathodes, nectarthodes, and lenticels), injuries and wounds (broken trichomes and lateral rots emergency), and by the entire surfaces.



**Figure 3.** View of the pineapple shell fruit cuticle in a low acid hybrid called MD2 (100 x magnification). The photo shows the shell cuticle's micro division in which the stomata, lenticels, and natural crack of the shell fruit are located—places of penetration of many pathogens (black circles).



**Figure 4.** Low acid hybrid pineapple fruits (MD2). The two photos show the symptoms of a pathogenic infection by *Fusarium* spp. 1) Evidenced penetration of the host possible through the shell stomata, lenticels, trichomes, and natural cracks (red circle). 2) Advance flesh infection where the pathogen already starts to eat and colonises the fruit (black circle)

#### Natural opening structures

The cuticle is the gateway between pathogens and plant tissue. This structure takes place in critical stages during the infection process (Melotto et al. 2008; Wibowo et al. 2014; Meeteren and Aliniaiefard 2016; Petkar and Ji, 2017; Rani and Greb, 2018; Singh and Sharma 2018). Furthermore, it is considered that some pathogenic and saprophytic microorganisms can survive and reproduce on the leaf surface without been exposed to infection (Melotto et al. 2008; Olvera-Carrillo et al. 2015; Meeteren and Aliniaiefard 2016; Thangavel et al. 2016). Although, many pathogenic fungi can penetrate the cuticle and epidermis using different paths (Mendgen et al. 1996; Meeteren and Aliniaiefard 2016; Singh and Sharma 2018). Some fungal diseases and pathogenic bacteria can enter and penetrate the host cuticle directly. Therefore, the cuticle represents a vital role in plant survival and tolerance against biotic and abiotic stresses (Mendgen et al. 1996; Meeteren and Aliniaiefard 2016; Nejat and Mantri, 2017; Zaynab et al. 2019; Prihatangsih and Soesanto, 2020). The main physiological role of the plant cuticle is to protect the tissue from a relatively dry atmosphere, thereby preventing dehydration by regulating water loss (Figure 3) (Kachroo and Robin, 2013; Meeteren and Aliniaiefard 2016; Domínguez et al. 2017; Singh and Sharma 2018).

Therefore, phytopathogenic bacteria can also enter their respective hosts via the stomata. It has been proven that after a heavy wind-rain, bacteria are randomly dispersed on the leaf surface; however, most promptly tend to disappear, except for those located near stomata (Huang 1986; Gudesblat et al. 2009; Pressel et al. 2014; Meeteren and Aliniaiefard 2016; Singh and Sharma 2018; Carriqui et al. 2019). In the stomatal cavities, bacteria multiply rapidly in mass before the infection can be visible to any unaided eye.

In addition, substomatal cavities function as shelters for bacterias (Huang 1986; Gudesblat et al. 2009; Misra and Chaturvedi, 2015; Meeteren and Aliniaiefard 2016; Singh and Sharma 2018). The bacterial masses arising from the substomatal cavities are trapped in polysaccharide slime filaments, and therefore the exuding bacteria works as inocula for a possible secondary infection (Huang 1986; Gudesblat et al. 2009; Spoel and Dong, 2012; Meeteren and Aliniaiefard 2016; Singh and Sharma 2018; David et al. 2019).

The position of the stomata between the surrounding and internal leaf tissues becomes another role for this microscopic pore. It provides a direct way for endophytic colonization of pathogens in plant tissues. Therefore, plants have established mechanisms to regulate stomatal opening, not only in response to harmful environmental factors, but also in response to pathogens (Melotto et al. 2008; Gudesblat et al. 2009; Shah and Zeier, 2013; Carella et al. 2016; Meeteren and Aliniaiefard 2016; Singh and Sharma 2018).

Wang et al. (2011), in research comparing two types of orange, *Meiwa Kumquat*, and *Newhall navel*, showed that stomatal characteristics may be the most important factor in citrus plants against bacteria. For that reason, they concluded that the existence of more stomata with larger opening areas on the surface of the fruit can increase the susceptibility to bacteria attacks.

It has been reported that the number of fruitlets or eyes of pineapple in the shell is arranged in eight long spirals. Also, the number of eyes ranged from 96 to 176, with an average of 141 (Rohrbach and Johnson 2003; Sipes and Pires de Matos 2018). These findings may explain why pineapple with a more significant number of eyes in the shell are more susceptible to a pathogen infection during



and after ripening compare to those with a lower number of eyes, because the eyes of the shell are the primary source of the stomata location and natural cracks of the fruit (Figure 4). However, this research topic needs to be studied further.

Hydathodes are another opening structure similar to stomata except that the protective cells attached to hydathodes cannot control the aperture and opening. The hydathodes are usually located in the marginal teeth or serrations of leaves; also, those exits in the leaf tips of *Brassica* and plants belonging to the *Gramineae*, *Crassulaceae*, and *Saxifragaceae* families (Huang 1986; Gudesblat et al. 2009; Chen et al. 2015; Meeteren and Aliniaefard 2016; Kim 2019). In these type of plants, water is excreted in the morning when the soil condition is wet, and transpiration is reduced due to high humidity, poor circulation of air, or the closing of stomata under reduced light (Huang 1986; Gudesblat et al. 2009; Bailey and Leegood, 2016; Meeteren and Aliniaefard 2016; Kim 2019).

The water droplets secreted by the hydathodes are taken to the surface by the veins' laticifers and pass through the intercellular spaces of the epithem. These water droplets are continually in contact with the liquids in the vascular system and can be drawn back into the leaf when the stomata opened, and transpiration is accelerated (Huang 1986; Gudesblat et al. 2009; Meeteren and Aliniaefard 2016; Kim 2019). Therefore, bacteria suspended in the water droplets can enter again into the plant by the vascular tissues' vicinity. The water droplets secreted from hydathodes contain amounts of substances that serve as chemical attractants and as nutrient sources for plant-pathogenic bacteria (Huang 1986; Gudesblat et al. 2009; Meeteren and Aliniaefard 2016; Kim 2019; Jauneau et al. 2020).

Like hydathodes, the nectarhodes are structures-like stomata that secrete nectar through the open tissue between the appearance of stems and the stamens (Huang 1986; Gudesblat et al. 2009; Meeteren and Aliniaefard 2016; Kim 2019; Zeng et al. 2020). Nectarhodes are formed by two guard cells comparable to leaf, and the stem stomata, except these cells, do not regulate the aperture and opening. A defined cuticle covers the entire nectarial surface. In addition, nectarhodes are the only places where the cuticular covering is interrupted (Huang 1986; Gudesblat et al. 2009; Meeteren and Aliniaefard 2016; Boucher et al. 2019; Kim 2019). Below the nectar region, there is a 12 to 15 cell deep area of the tissue in which nectar is produced, and many pathogens reproduce well in this tissue once it gains entrance (Huang 1986; Gudesblat et al. 2009; Meeteren and Aliniaefard 2016; Kim 2019).

In the pineapple fruit collapse, the responsible bacteria invade the ovary through the style, generating the water-soaked necrosis symptoms at the base of the stylar canal inside the fruitlet core (Huang 1986; Rohrbach and Johnson 2003; Tancos et al. 2017; Sipes and Pires de Matos 2018). However, the exact site of bacterial introduction has not been determined. Moreover, the bacteria remain viable but quiescent for about two months, and then break out to invade the entire fruit (Huang 1986; Rohrbach and Johnson 2003; Vrancken et al. 2013; Sipes and Pires de Matos

2018; Polsinelli et al. 2019).

The opening structure of lenticels consists mainly of the periderm of the stems and roots, usually under a stoma in the original epidermis. Lenticels usually develop from a stoma or a group and their most important function is related to gas exchange (Huang 1986; Gudesblat et al. 2009; Meeteren and Aliniaefard 2016; Singh and Sharma 2018; Khanal et al. 2020). During the transformation of stomata into lenticels, cells in the first two subepidermal cell layers close to the substomatal cavity separated in inward and outward directions. This separation results in creating a mass of loosely arranged parenchyma cells with massive intercellular spaces, with the majority of cell walls not being suberised (Huang 1986; Gudesblat et al. 2009; Meeteren and Aliniaefard 2016; Knoche and Lang, 2017; Singh and Sharma 2018).

Due to the continuity in the intercellular spaces and inner tissues, lenticels provide entry for several plant pathogens (Huang 1986; Gudesblat et al. 2009; Meeteren and Aliniaefard 2016; Khanal et al. 2019; Kim 2019). There are no sufficient documented studies about the incidence of diseases and the relationship to lenticel infection in pineapple plants and fruit. However, research in some fruits have been published, like in apple (Guan et al. 2015; Wenneker et al. 2017), mango (Rymbai et al. 2012), and pear (Wenneker et al. 2017).

#### Injuries and wound structures

There are other paths that pathogens have to penetrate the host, namely through injuries and wounds. Broken trichomes exhibit one of these possibilities. Trichomes are epidermal projections of diverse forms, structures, and functions (Huang 1986; Gudesblat et al. 2009; Meeteren and Aliniaefard 2016; Vacher et al. 2016; Amboden et al. 2018; Singh and Sharma 2018). They can be unicellular or multicellular, including or excluding secretory functions. Most of these trichomes are fragile and mostly collapse under slight pressure (Łaźniewska et al. 2016; Ma et al. 2016; Danovaro et al. 2017). The proportion of trichomes on leaf surfaces varies from species to species. In a single plant, most of the trichomes are discovered in younger leaves than in older leaves, and also more in the lower leaf surface than in the upper one (Huang 1986; Gudesblat et al. 2009; Ensikat et al. 2016; Meeteren and Aliniaefard 2016; Singh and Sharma 2018).

In pineapple and *Bromeliaceae* species, few studies have been developed to understand the function and impact of the trichomes on the quality of plants and fruits. Some studies have clearly shown that trichomes provide a function on an absorption of dissolved nutrients (Sakai and Sanford 1980; Meeteren and Aliniaefard 2016). Furthermore, another finding indicates that an essential ancestral function of the foliar trichome in *Bromeliaceae* plants is water repellency (Sakai and Sanford 1980; Meeteren and Aliniaefard 2016). As till, there is no enough information regarding pathogen disease incidences concerning the trichomes existence in the shell of fruit, although some authors have suggested an association to the dermal behavior of the fruit involved in skin conductance properties influencing the fruit transpiration (Montanaro et

al. 2012; Givnish et al. 2011; Givnish et al. 2014; Leroy et al. 2019).

In contrast, the emergence of lateral roots can provide another opportunity for pathogens to penetrate the host plant. These lateral roots usually originate from the pericycle and grow through the cortex of the parent root. Once the lateral root breaks through the outer epidermal layer to the outside, pathogens create an entrance by the resulting crevice (Huang 1986; Gudesblat et al. 2009; Meeteren and Aliniaiefard 2016; Vanhoutte et al. 2016; Carvalho et al. 2017; Silva et al. 2018; Wibowo et al. 2021). The space created by lateral-root formation is a representative avenue of entry for pathogens. After entering the root tissue, the bacteria spread rapidly by the intercellular space and finally invade the vascular bundles (Huang 1986; Gudesblat et al. 2009; Meeteren and Aliniaiefard 2016; Leroy et al. 2019).

### DISEASES RESISTANT MECHANISM IN HORTICULTURAL CROPS

Plants having a disease-resistant mechanism inhibit the growth of numerous pathogens (bacterial, fungal, or viral). This action is carried out in a restricted area around the initial infection point, where a wound is usually developed (Jupe et al. 2013; Wang and Balint-Kurti, 2015; Künstler et al. 2016; Goñi et al. 2017; Balint-Kurti, 2019; Kamanga et al. 2019). These mechanisms are achieved through a preventive controlled death cell, usually called hypersensitive reaction (HR). The HR can lead to acquired resistance (AR), defined as resistance to subsequent pathogen attacks, developed after the initial inoculation with lesion-forming in viruses, bacteria, and fungi (Kumar and Kirti 2015; Na et al. 2015; Chen et al. 2016; Goñi et al. 2017; Balint-Kurti, 2019). Subsequently, the acquired resistance can be subdivided into local acquired resistance (LAR), detected in the vicinity of the HR lesions, and systemic acquired resistance (SAR), detected in uninfected parts of the plants (Vlot et al. 2009; Van Doorn et al. 2011; Soesanto et al. 2011; Goñi et al. 2017; Birch et al. 2018; Balint-Kurti, 2019).

Previous studies reported that salicylic acid (SA), a second metabolite product of the plants, can promote SAR induction after a localized infection, and therefore becoming a type of long-distance communication mediator (An and Mou, 2011; Fu and Dong, 2013; Goñi et al. 2017; Radojčić et al. 2018). SA moves from infected areas of the plant to the uninfected ones by the phloem. This phenomenon was confirmed by using radiolabeled SA and its analogs (Hayat et al. 2010; Goñi et al. 2017). When SAR develops in a plant, it can be detected several days after the initial infection, lasts for several weeks, and it might be effective against a broad range of pathogens (even when they are unrelated to the initial infection) (Goñi et al. 2017).

Habitually, in association with HR and SAR, there is another plant response, the systemic synthesis of pathogenesis-related proteins (PRP) (Vlot et al. 2009; Soesanto et al. 2011; Dempsey and Klessing, 2012; Goñi et

al. 2017; Klessing et al. 2018). The localization, timing of appearance, and functions of at least some PRP suggest their involvement in the mechanisms of acquired resistance (Rivas-San Vicente, 2011; Lebeis et al. 2015; Vos et al. 2015; Goñi et al. 2017).

In previous research on the systematic acquired resistance in pineapple, a case applied to nematode infection was reported (*Meloidogyne javanica* and *Rotylenchulus reniformis*). In this case, it was discovered that foliar applications of acibenzolar-s-methyl (100-200 mg/L) induced SAR, compare to DL- $\alpha$ -amino-n-butyric acid (AABA), DL- $\beta$ -amino-n-butyric acid (BABA),  $\gamma$ -amino-n-butyric acid (GABA), p-aminobenzoic acid (PABA), riboflavin, and salicylic acid (SA). In addition, this had to be corroborated by the reduction in the number of nematode eggs when sprays of acibenzolar-s-methyl were used in pineapple inoculations (Walters et al. 2013; Mukhopadhyay, 2014; Goñi et al. 2017; Lu et al. 2019).

Hypersensitive reactions and SAR in pineapple diseases, such as fruit collapse or bacterial heart rot, are not well investigated as there is a lack of literature regarding the topic. Moreover, the mechanics on how HR, LAR and SAR are induced and activated in pineapple still need to be further studied and documented.

### CELL WALL ENZYMES, DISEASES AND *ERWINIA* FAMILY

Enzymes of bacterial origin can degrade plant cell walls. The production of a large number of enzymes that degrade the cell wall by phytopathogenic bacteria is largely documented (Marín-Rodríguez et al. 2002; Bellincampi et al. 2014; Daher and Braybrook, 2015; De Freitas and De Cássia 2017; Cosgrove, 2018).

During the initial stage of infection, the pathogens secrete pectolytic enzymes that degrade pectins in the host cell wall, allowing the pathogen to spread the infection in the cell membranes (Toth et al. 2011; Schwartz et al. 2015; De Freitas and De Cássia 2017; Motyka et al. 2017; Yilmaz et al. 2019; Soesanto, 2020). One of the secreted enzymes is known as Pectate Lyases (PL). Furthermore, pectate Lyases catalyze the eliminatory cleavage of de-esterified pectin, representing an essential component of many higher plants' primary cell walls (Marín-Rodríguez et al. 2002; Bellincampi et al. 2014; Hugouvieux-Cotte-Pattat et al. 2014; De Freitas and De Cássia 2017; Ke et al. 2018; Wang et al. 2018). PL cleavage requires the existence of calcium ions and oligosaccharides with unsaturated galacturonosyl residues at their non-reducing ends (Marín-Rodríguez et al. 2002; Bellincampi et al. 2014; Dubey et al. 2016; Uluisik et al. 2016; De Freitas and De Cássia 2017; Soesanto et al. 2020).

It was concluded that PL was produced primarily by plant pathogens and that their action can cause the maceration of plant tissues. However, the large number of PL-like sequences in plant genomes exposed a significant role for these enzymes in various plant development processes (Marín-Rodríguez et al. 2002; Soesanto et al. 2013; Bellincampi et al. 2014; De Freitas and De Cássia



2017; Paniagua et al. 2017; Yang et al. 2017).

The pectate Lyases activity was first discovered in 1962 in cultures of *Erwinia carotovora* and *Bacillus* sp. (Marín-Rodríguez et al. 2002; Joko et al. 2018) and their secretion by phytopathogenic bacteria have been well-documented (Marín-Rodríguez et al. 2002; Bellincampi et al. 2014; De Freitas and De Cássia 2017). The effect of pectate lyases not only leads to the deterioration of the plant cell wall degradation but also to the activation of defense systems. These defensive mechanisms can be generated by the release of oligogalacturonides from the plant cell wall, which subsequently acts as defense elicitors (Marín-Rodríguez et al. 2002; Bellincampi et al. 2014; De Freitas and De Cássia 2017; Soesanto et al. 2020).

In conclusion, fruit collapse and bacterial heart rot diseases are caused by the pathogen *Erwinia chrysanthemi* (currently classified as *D. zea*). The physical symptoms of fruit collapse are juice, the release of gas in the form of bubbles, and the olive-green color of the fruit shell. Meanwhile, bacterial heart rot is characterized by water-soaked zones on the centermost leaves surrounding the apical meristem, formation of brown streaks on the lamina and in mesophyll tissues, and a light-brown exudate emerging from the blisters as leaves begin to rot.

It is necessary to understand the media and how the pathogen penetrates into the plant and fruit through its ultrastructure. In pineapple plant, *D. zea* focuses on host tissue penetration determined by the plant's natural opening, lesions, and injuries, and mainly during the opening phase of flowering weeks prior to harvest. Consequently, it is important to further study and evaluate the defense mechanisms in these infectious diseases of pineapple plants and fruit from a cellular and enzymatic level, taking into account the hypersensitive reactions, local and systematic acquire resistance. This information can help determine which type of treatments effectively prevent the pathogen attack and what is expected to be carried out in order to control the disease once the infection has occurred. The review presented here can serve as a future reference in order to determine the causes of bacterial heart rot and fruit collapse, identify the symptoms, and the factors that influence pineapple susceptibility.

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