

Calla lily soft rot causal agents, symptoms, virulence and management: a review

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Summary: Bacterial soft rot is a polyetiological disease attacking calla lily [*Zantedeschia spp* (L.) Spreng.]. This disease has reduced the commercial value of this crop. This work aims to review scientific information to give an insight into calla lily soft rot causal agents, symptoms, factors favouring the disease, virulence mechanisms and management strategies. Special emphasis is put on the current progress with regards to understanding calla lily mechanisms of resistance to soft rot and their potential for the development of tolerant/resistant cultivars with commercial traits.

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Introduction

Calla lily is one of the most economically important cut flowers. There are eight species of calla lily, divided into two sections: *Zantedeschia* and *Aestivae*. Calla lilies in the *Zantedeschia* section have white flowers while those in the *Aestivae* section have a variety of colours. Consequently, there are several varieties of calla lily used as cut flowers and pot plants depending on the flower shape and colours (Jonytiené et al., 2017) and the vase life (Lazzereschi et al., 2011). Commercially, calla lily is one of the major cut flowers traded on the international market. In the year 2014, it ranked 15th in the top 25 cut flowers and indoor plants sold in the Dutch auction (FloraHolland, 2014). Despite this ranking, the commercial importance of this flower has been declining globally (Cho et al., 2014). Currently, it is not classified among the top cut flowers and indoor plants sold in the Dutch auction (FloraHolland, 2020). Statistics from New Zealand which has been the leading exporter of calla lily flowers and tubers have shown a decline in total revenue generated by this flower from 7.7 million \$ (fob) in 2000 to 0.3 million \$(fob) in 2019 (Aitken & Warrington, 2019).

The major reason for the decline in commercial importance of calla lily is the soft rot disease caused by pectolytic bacteria. This disease reduces the yield and quality of flowers. Soft rot had previously led to the decline in demand, production and breeding of calla lilies in the 1960s and 1970s (Kuehny, 2000). However, calla lily production got revived with the development of cultural practices for the prevention and suppression of soft rot disease infestation as well as the development of tissue culture and true F1 seed lines (Kuehny, 2000). Despite the application of the cultural methods in combination with the application of antibiotics, the disease continued to affect calla lily production thereby decreasing its area under production and commercial value (Cho et al., 2014).

Since calla lily produced from seeds or tissue culture has a long juvenile phase, its commercial production relies on tubers and rhizomes. However, soft rot bacteria are endemic in soil and their control cannot be achieved by planting clean tubers (Cho et al., 2014; Snijder & Van Tuyl, 2002). Moreover, tubers may have a latent infection which may be unnoticed until conditions favouring the disease prevail. Other factors such as the unavailability of an effective antibiotic, the wide range of alternate hosts, several bacteria species causing the disease and the virulence of this disease make control measures difficult to implement (Cho et al., 2014). The disease is considered a “cancer” in calla lily production, particularly in the *Aestivae* section (Wu et al., 2017). Therefore, there is a need for research focused on identifying the disease causal agents and mechanisms of virulence, understanding crop resistance to this disease to develop resistant varieties and alternative control measures that can be integrated with the existing practices for effective management. This review provides an extensive description of the soft rot in calla lily. It explores the reported causal agents, factors favouring the diseases, control measures and the tolerance and resistance mechanisms of calla lily to soft rot. It also examines the breeding for resistance of calla lily against soft rot with emphasis on the potential use of genetic modification as a way forward.

Causal agents

Calla lily soft rot has been for a long time thought to be caused by *Pectobacterium carotovorum* formerly known as *Erwinia carotovora* (Cho et al., 2014; Krejzar et al., 2008; Ni et al., 2010; Wright & Triggs, 2009). However, there have been reports of other pectolytic bacteria causing the soft rot disease. The other bacteria that have been reported to cause soft rot in calla lily include *Chryseobacterium indologenes* (Mikiciński et

al., 2010), *Pectobacterium chrysanthemi* (formerly *Erwinia chrysanthemi*) (Lee et al., 2006), *Pectobacterium brasiliense* (Guttman et al., 2021; Khadka et al., 2020), *Pectobacterium zantedeschiae* sp. nov. (Waleron et al., 2019), *Pectobacterium atrosepticum* (Mikiciński et al., 2010; Popovic et al., 2017), *Pectobacterium aroidearum* (Guttman et al., 2021), *Pseudomonas marginalis* (Krejzar et al., 2008; Mikiciński et al., 2010), *Pseudomonas putida* (Krejzar et al., 2008), *Pseudomonas veronii* (Mikiciński et al., 2010), *Paenibacillus polymyxa* (Mikiciński et al., 2010) and *Dickeya dadantii* (Guttman et al., 2021).

Symptoms of calla lily soft rot

Calla lily soft rot is a disease that can occur throughout all growth stages from the field to storage. Its infection does not always result in symptoms. The infection is sometimes latent. As the disease progresses, the plant first turns yellow, produces a foul smell (Snijder et al., 2004a, 2004b), develops water-soaked lesions on leaves and stems (Popovic et al., 2017) and becomes completely macerated (**Figure 1**) resulting in a total collapse of the plant and death in a few days (Mikiciński et al., 2010; Snijder et al., 2004a, 2004b).

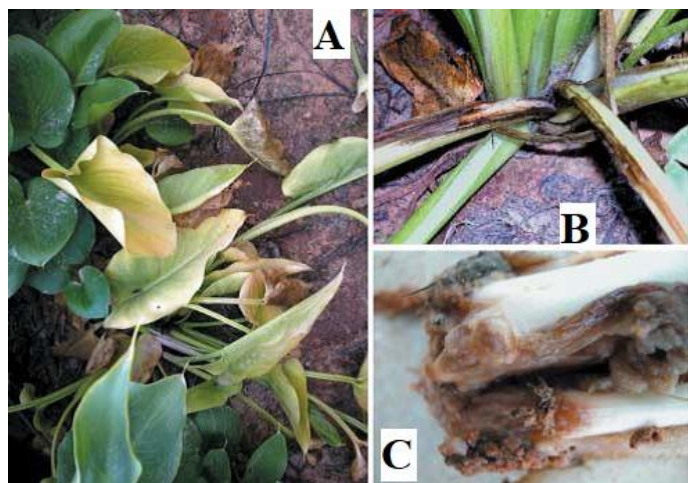


Figure 1. Symptoms of soft rot on calla lily (A) Discoloration of leaves; (B) Rotting leaf petioles; (C) Tuber and leaf base rot (Luzzatto et al., 2007b)

Factors favouring the calla lily soft rot disease

Calla lily soft rot is mainly affected by anaerobic incubation, inoculation, temperature and wounding of calla lily tubers. These factors have been classified in the order of significance considering how they affect the disease score. Temperature has the greatest effect on calla lily soft rot score followed by wounding tubers. The inoculation with the soft rot-causing bacteria is in the third position while incubation in anaerobic conditions (or reduced oxygen conditions) comes last (Wright & Triggs, 2009). According to a study by Wright and Triggs (2009), tubers which were not wounded nor inoculated with *Pectobacterium carotovorum* and incubated at 30 °C developed rots. The increase in temperature resulted in an increased disease score. At 20 °C, the majority of calla lily tubers did not show symptoms while at the temperature of 30 °C, the majority of tubers had soft rot symptoms. High temperature can induce severe calla lily soft rot from latent infection. Wounding facilitates the entry of soft rot-causing bacteria that already present in the growing media or at the surface of calla lily tubers.

It also facilitates the infection of symptomless tubers by calla lily soft rot bacteria. It releases nutrients necessary for the soft rot bacteria present in latent state in calla lily tubers lenticels (Wright & Triggs, 2009). Once established, bacteria multiply until they reach the quorum that can initiate the disease. This infection is greatly enhanced by wounding and high-temperature conditions that impair the host resistance and favour the multiplication of the bacteria. Moreover, under anaerobic conditions, fewer number bacteria are needed to initiate the calla lily soft rot disease than in aerobic conditions (Wright & Triggs, 2009).

Another factor that attracts attention is crop nutrition. Experiments conducted by Gracia-Garza et al. (2004) revealed that phosphorus nutrition greatly affects the soft rot infection. The addition of phosphorus fertilizers in the soilless medium increased the soft rot incidence by 51% in comparison to regular soil mix without superphosphate application. However, the addition of superphosphate in the nutrient solution met the plants' needs without increasing the incidence of soft rot. Laboratory experiments demonstrated an increase in soft rot development in tubers treated with a suspension of *Pectobacterium carotovorum* prepared in a solution of KH_2PO_4 . The increased soft rot in the presence of phosphorus may be a result of increased enzymatic activity of polygalacturonase and pectate lyase. The application of phosphorus stimulates root formation which leads to sequential wounding. These wounds facilitate the entry of soft rot-causing pathogens. However, the increased incidence of soft rot disease in the presence of phosphorus depends on the virulence of the *Pectobacterium* and not the increased susceptibility of the tuber (Gracia-Garza et al., 2004).

Virulence mechanisms

Calla lily soft rot-causing bacteria are considered opportunistic pathogens. They cause the disease when conditions which impair the host resistance and favour the pathogen multiplication are available (Wright & Triggs, 2009). Soft rot bacteria enter calla lily plants through natural openings like lenticels (Wright & Triggs, 2009). They establish themselves in the intercellular spaces at the infection sites and then start multiplying until they reach the critical number. Once this critical number is reached they produce and excrete extracellular enzymes which are collated with their virulence (Ni et al., 2010).

To model the expression of genes of virulence of soft rot-causing bacteria after infecting calla lilies, Fan et al. (2020) conducted a study on *Pectobacterium carotovorum* subsp. *carotovorum* PccS1. This study revealed that the expression of *Pectobacterium carotovorum* subsp. *carotovorum* PccS1 genes varies depending on functional categories. Their expression demonstrates a consistent pattern of regulation during the infection (Fan et al., 2020). Most significantly and differentially expressed genes encoding proteins in the membrane transport are upregulated while those for carbohydrates are downregulated. Half of the genes for metabolism are upregulated while the other half are downregulated (Fan et al., 2020). Proteins that are upregulated are probably involved in bacterial-plant interaction and bacterial multiplication. Hence, they represent genes involved in *Pectobacterium carotovorum* colonisation and adoption to different levels. *Pectobacterium carotovorum* uses the metabolic pathways from sucrose/glucose and pectin to acetyl-Coa via pyruvate as its carbon pathways during infection (Fan et al., 2020).

The appearance of soft rot disease in calla lily is a manifestation of numerous enzymes degrading the cell membrane and the cell wall. Pectolytic bacteria excrete cellulases, pectinases, proteases, phospholipases and xylanases which degrade the cell wall and the membrane components (Gracia-Garza et al., 2004). The synthesis of these plant cell wall degrading enzymes and other virulence determinants by soft rot bacteria is mediated by quorum sensing (Joshi et al., 2016a; Monson et al., 2019).

Soft rot-causing bacteria use 3-oxohexanoyl-L-homoserine lactone and 3-oxooctanoyl-L-homoserine lactone as signalling molecules. The cell-dependent expression of plant cell wall degrading enzymes in *Pectobacterium* is regulated by the *expI-VirR*. The *expI* is an acyl-homoserine lactone synthase which produces freely diffusible signalling molecules detected by the gene *expR* thus affecting the synthesis of plant cell wall degrading enzymes (Joshi et al., 2016b). This quorum sensing network regulating virulence responds to genes related to acyl-homoserine lactones such as *carI* and *expR*. It is also regulated by pectin catabolism genes such as *kdgR*, *rsmA* and *rsmB* (Fan et al., 2020).

The genome of *Pectobacterium* contains pectinase encoding genes. The majority of them are upregulated when it infects calla lily. These include genes for pectate lyase, polygalacturonase, pectin methyl and pectin-acetyl-esterase. The majority of pectate lyase genes in *Pectobacterium* are upregulated when it infects calla lily demonstrating their importance in the infection. Other crucial genes such as *rply*, *eda*, *hfq*, and *flgK* affect the activities of plant cell wall degrading enzymes. For instance, the gene *rply* is induced by plant extract of *Zantedeschia elliotiana* showed that its deletion leads to reduced plant cell wall degrading enzymes (Jiang et al., 2017). The gene *hfq* is also important for the virulence of *Pectobacterium carotovorum* PccS1. Mutation of the *hfq* gene from *Pectobacterium carotovorum* subsp. *carotovorum* leads to reduced virulence and plant cell wall degrading enzymes (Wang et al., 2018). The upregulation or downregulation of these genes depends on the strain, the environmental nutrient status and the duration of infiltration in the host (Fan et al., 2020).

In studying the virulence strains with a mutation in one differently expressed gene, Fan et al. (2020) revealed that *Pectobacterium carotovorum* uses the T3SS gene to induce plant cell death rather than maceration of plant tissue directly. The maceration of plant tissues following the soft rot bacteria is due to the depression of callose deposition in the plant for resistance by the pathogenesis-related genes and the superlytic ability of pectinolytic enzymes produced by *Pectobacterium carotovorum*. It is worthy to note that the majority of available literature focused on the virulence mechanisms employed by *Pectobacterium carotovorum*. Therefore, studies that would enable the understanding of the virulence of other bacteria causing soft rot on calla lily should be the focus of the scientific community.

Management of calla lily soft rot

Cultural methods for soft rot management

The management of calla lily soft rot encompasses several management methods. The first step consists of using disease-free planting materials and avoiding the use of wounded calla lily tubers. Wounded calla lily tubers are predisposed to calla lily soft rot infection. The removal of infected plants halts the transmission of soft rot disease from infected surfaces to non-infected ones. When applied, this practice systematically

reduces the disease score. Its efficiency is much improved by dipping tubers for 15 minutes in an aqueous solution of 0.08 copper hydroxide, 0.12% thiram and 0.03% benomyl before planting and the use of mulch (Wright et al., 2005b).

The second cultural method used for soft rot management is mulching. The use of mulching not only contributes to suppressing weeds growth but contributes to conserving the soil moisture (Wright & Burge, 2000) and reduces temperature fluctuation within the soil (Lee et al., 2019; Wright & Burge, 2000). It also manages plant diseases by reducing soil splashing of primary inoculum. It influences the moisture content and temperature of the soil and enhances the soil microbiological activity that suppresses soil-borne plant pathogens (Wright & Burge, 2000). Given that the anaerobic conditions favour the disease, organic mulch allows better drainage which increases oxygen circulation.

Adequate provision of soil moisture is essential in calla lily production. Water contributes to the spread of soft rot bacteria from surfaces of infected tissues to those of healthy ones. Excessive water supply increases the incidence of calla lily soft rot by increasing the succulence of plant tissues which are in turn predisposed to plant diseases and creating waterlogged conditions within the soil and reducing the available oxygen in the soil. Water deficit also facilitates the occurrence of soft rot because it weakens the plant (Wright & Burge, 2000). Results of a study by Wright and Burge (2000) proved that the incidence and severity of calla lily soft rot in mulched and irrigated calla lily plants were 15% less than in irrigated calla without mulch or mulched calla without irrigation. Mulching reduces the soil temperature which in turn reduces the incidence of soft rot.

The reduction of temperature is crucial in the management of soft rot. Treatments that lower the soil temperature considerably reduce the incidence and severity of calla lily soft rot. In this regard, shading which is used to enhance the quality of calla lily cut flowers plays the role of reducing the temperature in the production area. This results in the reduction of calla lily soft rot incidence (Nam et al., 2012).

Nutrition is very important in calla lily soft rot management. Addition of phosphorus fertilizers in the growing medium contributes greatly to increased soft rot incidence. However, the addition of phosphorus fertilizers in nutrient solution can meet the calla lily phosphorus needs without enhancing the soft rot. Hence, it is recommended to supply phosphorus in a nutrient solution rather than applying it to growing media (Gracia-Garza et al., 2004).

Chemical control of calla lily soft rot

Chemical methods have been used as means for the control of calla lily soft rot. Several products have been tested to control calla lily soft rot. They include streptomycin, copper-based products, sodium hypochlorite and formaldehyde. Dipping tubers in 200 ppm streptomycin for 30 minutes proved to be effective against *Pectobacterium carotovorum* (Kuehny et al., 1998). However, due to the development of resistance by soft rot bacteria (Charkowski, 2018), it was necessary to find alternatives to antibiotics that could control calla lily soft rot. Copper-based products were therefore evaluated as options to control calla lily soft rot.

In vitro study revealed that copper-based products suppress soft rot-causing bacteria. Their efficacy was, however, reduced when there was phosphate in fertilizer solutions. Pre-plant applications of copper reduce infection caused by soft rot bacteria (Gracia-Garza et al., 2002). However, this effect fades

within 6 weeks after establishment or is not significant (Blom & Brown, 1999). The lack of significant effect of pre-plant application after crop establishment may be due to the presence of bacteria-causing soft rot in the epidermis of the tuber and the inability of the copper-based products to penetrate into the tuber (Blom & Brown, 1999). Post planting application of copper-based products (copper hydroxide 24.4%, copper oxychloride 50% metallic copper and copper hydroxide 53.8%) is effective in controlling calla lily soft rot (Gracia-Garza et al., 2002). These compounds are effective when applied in overhead irrigation, sub-irrigation (Gracia-Garza et al., 2002) or when drenched (Wright et al., 2005a). The post-planting applications reduce the secondary infection that may occur in closed irrigation systems (Gracia-Garza et al., 2002). Despite being effective against calla lily soft rot, both pre-planting and post-planting application of copper-based products have a phytotoxic effect on calla lilies. They reduce the number of flowers produced (Blom & Brown, 1999; Gracia-Garza et al., 2002). The phytotoxicity on calla lily leads mainly to the reduction of roots growth (Gracia-Garza et al., 2002). Moreover, the effectiveness of copper-based compounds is reduced by the presence of phosphate ions in fertilizer solutions as it is speculated that copper compounds are bound by phosphates ions in fertilizers solution (Gracia-Garza et al., 2002).

Biocontrol of calla lily soft rot

With the development of resistance of calla lily soft rot to streptomycin and the toxicity of copper-based products on calla lily, efforts have been oriented towards finding products that are environmentally friendly and effective against calla lily soft rot. In this regard, the use of endophytic bacteria that can colonise the tissues of plants without damaging the hosts is being explored as an alternative to chemical pesticides. *Bacillus amyloliquefaciens* (Azaiez et al., 2018) and *Myxococcus spp* (Li et al., 2018) have shown some efficacy against calla lily soft rot bacteria. *Bacillus amyloliquefaciens* strain Ar 10 produces glycolipid-like compounds that exhibited potent antagonist activity against *Pectobacterium carotovorum*. It demonstrated a killing rate of 94.6% to 96% of *Pectobacterium carotovorum* and reduced the severity of soft rot disease symptoms (Azaiez et al., 2018). *Myxococcus spp* have shown that they can control soft rot bacteria by predation, promotion of calla lily growth and production of progeny tubers without disease despite the existence of the soft rot disease in the mother tubers (Li et al., 2018).

Application of phenolic acids has also been explored as an option to control calla lily soft rot. The application of cinnamic acid and salicylic acid reduces the virulence of soft rot bacteria by interfering with the quorum sensing system (Joshi et al., 2016a). Exposure of *Pectobacterium aroidearum* and *Pectobacterium brasiliense* to non-lethal concentrations of cinnamic acid and salicylic acid inhibits the expression of quorum sensing genes such as *expl*, *expR*, *PC-1442* and *luxS*. Similarly, volatile essential oils such as carvacrol and eugenol have shown the capacity of interfering with the quorum sensing system of soft rot bacteria (Joshi et al., 2016b). The inhibition of the quorum sensing impairs the biofilm formation and plant cell wall degrading enzymes thereby reducing the infection.

Plant extracts have also been explored for calla lily soft rot control. Extracts from *Coptis chinensis* demonstrated antibacterial activity against *Pectobacterium carotovorum subsp. carotovorum* (Githeng'u, 2015; Githeng'u et al., 2015). Laboratory experiments demonstrated that *C. chinensis* at 100%

concentration produced an inhibition zone comparable to that of streptomycin sulphate (Githeng'u et al., 2016). Drench application of extracts from *Coptis chinensis* at the rate of 2.51 ha⁻¹ significantly reduced the soft incidence in calla lily 'Black magic'. Application of these extracts at the full foliage stage had no significant effect on the incidence of the disease. Berberine chloride present in *Coptis chinensis* has strong antibacterial bioactivities (Githeng'u et al., 2015).

Meta-coumaric and trans-cinnamic compounds extracted from Chilli (*Capsicum annum* L.) inhibit the growth of *Pectobacterium carotovorum*. Capsaicin and dihydrocapsaicin did not affect the growth of this bacterium. This further confirms the effect of cinnamic acids (Joshi et al., 2016a) as highlighted above. Despite the efficacy demonstrated by these biological products, their application has not been explored at the commercial level.

Tolerance and resistance against calla lily soft rot

So far the control of calla lily soft rot is difficult. Currently, it is recommended to combine different cultural practices, chemical control and resistant varieties (Cho et al., 2014). Nevertheless, coloured cultivars of call lily with high ornamental value are highly susceptible to bacterial soft rot. The scientific community concurs that calla lily varieties belonging to the *Zantedeschia* section exhibit better resistance to bacterial soft rot (Cho et al., 2014; Wu et al., 2017). However, some cultivars in the section *Zantedeschia* have shown some level of susceptibility to calla lily soft rot (Cho et al., 2013, 2014; Joung et al., 2013). Understanding mechanisms of resistance of calla lily against soft rot is, therefore, very important for breeding new cultivars with good market prospects and resistance to calla lily soft rot (Wu et al., 2017).

Evaluation of calla lily resistance against bacterial soft rot

In a breeding program aimed at developing cultivars of calla lily resistant to bacterial soft rot, it is essential to identify variations in and genetics of resistance (Cho et al., 2013; Snijder & Van Tuyl, 2002). Moreover, it is recommended to use resistant/tolerant varieties. Therefore, methods of evaluating and categorizing calla lily cultivars for their resistance to bacterial soft rot are of paramount importance (Cho et al., 2013). Four methods have been tested to evaluate the resistance of calla lily against bacterial soft rot (Cho et al., 2013; Snijder & Van Tuyl, 2002). These methods include the whole tuber/rhizome method, the tuber/rhizome slice method, the leaf disk method and the petiole method.

For the whole tubers/rhizome method, tubers/rhizomes of calla lily are disinfected by washing them in tap water followed by immersion in 1% hypochlorite for 20 minutes and rinsed in tap water. These tubers/rhizomes are wounded at the base and inoculated with 20µl (1x10⁷cfu ml⁻¹) of the soft rot bacteria. The inoculated tubers are then incubated in 100% relative humidity and 20°C with their apical meristem pointed downwards (Snijder & Van Tuyl, 2002). For the tuber/rhizome slices method, tubers and rhizomes undergo the same cleaning and disinfection process. Tubers/rhizomes are cut into slices of 7-9 mm thick longitudinally using a clean knife. They are then inoculated by placing a piece of conventional laboratory paper soaked with 1x10⁵cfu ml⁻¹ of the soft rot bacteria in the middle of the cut surface. These slices are put in a layer of water approximately 1-2 mm deep with the inoculated side always facing up to prevent drying of the cut surface (Figure 2). The incubation

conditions are similar to those used in the tubers/rhizomes method. The measurement of resistance starts from the second day up to the sixth day. It consists of measuring the weight before and after washing away the infected tissues (Snijder & Van Tuyl, 2002).



Figure 2. Tuber slice test method. Tuber slices placed on the layer of sterile water-soaked lab paper (Cho et al., 2013).

The leaf disk method consists of making leaf disks of 20 mm from young leaves of newly sprouting plants using a cork borer. These disks are transferred to a well plate in 5 ml containing 1×10^7 cfu ml^{-1} of inoculum of the soft rot bacteria (**Figure 3**). These inoculated disks are kept in an environmental chamber maintained at 20°C and 100% relative humidity. Observations are made from the third day up to the sixth day and they include estimating the percentage of the macerated area (Snijder & Van Tuyl, 2002).

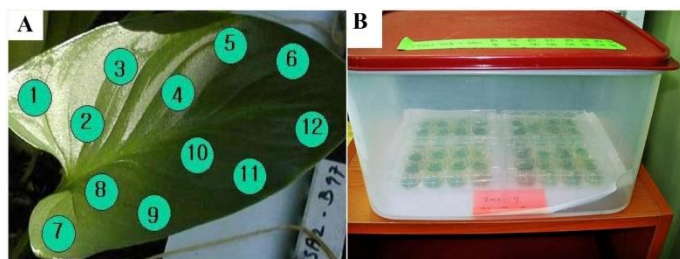


Figure 3. Leaf disk test method.

(A) The leaf punching position of the *Zantedeschia* leaf of the leaf disk test.
(B) Leaf disks submerged in the bacterial inoculum (Cho et al., 2013).

For the petiole test, the oldest leaves of plants are cut around flowering time using a knife. These leaves are disinfected in 80% ethanol. Immediately after disinfection, leaf blades are discarded. Petioles cut 20 cm from the top are washed three times in sterile water and surface dried. Petioles are then placed into a plastic tube of 2.0 cm containing 5 ml inoculum (1×10^5 cfu ml^{-1}) of the soft rot bacteria (**Figure 4**). They are then incubated in an environment chamber at 100% relative humidity for five days. The length of the healthy tissue is then measured to the nearest 0.5 cm (Snijder & Van Tuyl, 2002).

Among the four methods, the leaf disks and tuber or rhizome slices methods are recommended because of their reproducibility. The leaf disk method is recommended for evaluating the resistance of calla lily seedlings to calla lily soft rot. The tuber/slice method is recommended for assessing the resistance of cultivars at later growth stages. The whole tuber/rhizome and the petiole methods are not recommended because of their low reproducibility and being highly destructive

(Cho et al., 2013; Snijder & Van Tuyl, 2002). Currently, there is no agreed classification of calla lily cultivars based on their level of resistance to soft rot. Using leaf disk maceration percentage, Cho et al. (2013, 2014) proposed that calla lily cultivars can be classified as follows: cultivars with 1-10% leaf disk maceration are resistant, 11-30% are moderately resistant; 31-90% are susceptible while 91-100% are very susceptible. Joung et al. (2013) proposed the use of a disease index where 0 is assigned to those cultivars whose disks are not macerated, 1 is assigned to those cultivars whose disks developed symptoms on less than 25 mm^2 , 2 to those that develop symptoms on 25-50 mm^2 , 3 to those that develop symptoms on 51-150 mm^2 , 4 to those that develop symptoms on 151-250 mm^2 and 5 to those that develop symptoms over 250 mm^2 . For the classification, Joung et al. (2013) proposed that cultivars with an average disease index of 0-2 are classified as resistant, 2.0-3.5 be classified as moderately resistant and those of 3.5-5 be classified as susceptible.



Figure 4. Petiole test.

Petioles of calla lily placed in tubes (Cho et al., 2013).

Ecological adaptations leading to enhanced resistance of calla lily against soft rot

The possibility that ecological adaptations play a role in the tolerance/ resistance to calla lily soft rot exhibited more by calla lily cultivars in the *Zantedeschia* section than in the *Aestivae* section has been explored in a study reported by Guttman et al. (2021). This study revealed that *Zantedeschia aethiopica* possesses lower tissue compactness and higher content of air spaces in the mesophyll tissue. The environmental survival, establishment and spread of plant bacterial diseases are majorly influenced by the plant canopy. Transverse sections of leaves and petioles displayed larger air spaces occupying more parenchyma space in *Zantedeschia aethiopica*. Parenchyma tissues of *Aestivae* section calla lilies are compact. The difference in the petiole airspace of calla lily in the *Zantedeschia* section is almost double that in the *Aestivae* plants. Though there is no difference in the adaxial leaf surface of both *Aestivae* calla lily and *Zantedeschia* sections, there is a clear difference in the abaxial surfaces of the leaves. Leaves of calla lily in the *Zantedeschia* section have a smoother surface on their abaxial surface while those in the *Aestivae* section have a ridged rough pattern on their abaxial surface (Guttman et al., 2021). The colonisation of *Pectobacterium* cells is dense on the abaxial leaf surface of *Aestivae* calla lilies. *Pectobacterium* cells on the abaxial leaf surface of *Zantedeschia* section calla lily are scattered. These ridges and grooves which are typical on the coloured calla lily hybrids support the establishment of the soft rot bacteria.

Considering the origin of calla lily in the two sections, it is believed that these two adaptations resulted from ecological adaptations. The origin of a calla lily in the *Zantedeschia* section is confined to the southern coastal belt at an altitude up to 1000 m of marshy wetlands. Calla lily species of the *Aestivae* section originated from the mountainous regions at an altitude of above 1200 m and up to 2000 m. Hence, smoother leaf surfaces and larger airspaces of the aerenchyma in leaves are morphological features which are part of habitat adaptation associated with wetlands and the marshy valley of lower altitude where *Zantedeschia aethiopica* originates. The *Aestivae* section calla lily plants developed features such as condensed tissue and compact life form which is typical for higher altitudes. Since these features impact oxygen availability, it is clear that anaerobic conditions caused by condensed tissues in the *Aestivae* section of calla lilies favour the soft rot disease. Under anaerobic conditions, even low levels of soft rot bacteria can cause the disease. Hence, when bacteria that are already attached to leaves of *Aestivae* calla lilies penetrate them through natural openings or wounds they cause the soft rot disease because of anaerobic conditions. Oxygen-dependent host defences cell lignification and suberisation and the production of pectic enzymes are also affected by the dense and compact tissues of *Aestivae* calla lilies. Larger airspaces observed in *Zantedeschia aethiopica* contribute to their resistance against *Pectobacterium carotovorum* (Guttman et al., 2021).

Biochemical mechanisms of calla lily resistance

Defence mechanisms employed by calla lily species in response to *Pectobacterium spp* attack involve the systemic acquired resistance and the induced systemic resistance signalling pathways (Guttman et al., 2021; Wu et al., 2017). The systemic acquired resistance depends on the salicylic acid signalling pathway while the induced systemic resistance depends on the jasmonic acid signalling pathway (Wu et al., 2017). The resistance to soft rot exhibited by the *Zantedeschia aethiopica* is attributed to increased levels of salicylic acid, polyphenol oxidase and peroxidase after infection. Results of a study by Wu et al. (2017) revealed that salicylic acid levels increased 3 to 30 hours after infection by *Pectobacterium carotovorum*. Salicylic acid levels rose by 3.771 to 14.974 times compared to the control for *Zantedeschia aethiopica* while its increase in *Zantedeschia elliotiana* 'Florex Gold' was 2.64 to 6.35 times (Wu et al., 2017). Levels of polyphenols oxidase which were initially higher in *Zantedeschia aethiopica* also increased by 1.774 fold as compared to *Zantedeschia elliotiana* 'Florex Gold' which had its polyphenols oxidase levels increased by 1.4279 fold following infection by *Pectobacterium carotovorum* (Wu et al., 2017). Polyphenols oxidase oxidise phenolic compounds into quinones which in turn kill the pathogen (Wu et al., 2017). The activity of peroxidases increased in both resistant *Zantedeschia aethiopica* and susceptible *Zantedeschia elliotiana* 'Florex gold' after infection by *Pectobacterium carotovorum*. However, the increase in peroxidases was 5.5898 fold in *Zantedeschia aethiopica* compared to 2.8020 in *Zantedeschia elliotiana* 'Florex gold' (Wu et al., 2017). In another study, *Zantedeschia* hybrid 'Captain Romance' had higher initial levels of peroxidases compared to *Zantedeschia aethiopica*. However, these peroxidase levels in *Zantedeschia* hybrid 'Captain Romance' were downregulated after the infection by *Pectobacterium brasiliense* while they were upregulated in *Zantedeschia aethiopica* after the infection by the same bacteria (Guttman et

al., 2021). This may suggest that levels of the basal level of peroxidases are associated with the genetic make-up of the cultivar. Higher peroxidase levels are an important defence mechanism against pathogens. These protective enzyme systems scavenge the reactive oxygen species and protect the plant from pathogens' attacks (Guttman et al., 2021; Wu et al., 2017).

In *Zantedeschia aethiopica*, the application of elicitors triggers the resistance against *Pectobacterium carotovorum*. Benzothiadiazole, B-aminobutyric acid and methyl jasmonate have been used as elicitors (Luzzatto et al., 2007b, 2007a). The first two are involved in signal transduction pathways involving salicylic acid. Methyl jasmonate, on the other hand, is involved in the jasmonate/ethylene signalling pathway. Drench application or foliar applications of elicitors involved in salicylic acid pathway transduction reduced the soft rot disease symptoms and the proliferation of soft rot bacteria. However, the protection induced does not last. On the other hand, the application of methyl jasmonate completely inhibits soft rot bacteria development in calla lily leaves (Luzzatto et al., 2007b; Yedidia et al., 2011). This inhibition is attributed to augmenting the induction of polyphenols oxidases in treated leaves of the calla lily. The application of these elicitors on *Zantedeschia aethiopica* triggers the expression of proteins. Some proteins are up-regulated while others are downregulated. Some proteins associated with oxidoreductase activity are among those primed proteins. Oxidoreductases include hydroxylases, oxygenases, phenoloxidases and reductases (Luzzatto-Knaan et al., 2014). Plant induced with methyl jasmonate without infecting them with *Pectobacterium carotovorum* had two-fold increases in polyphenols oxidase. In the infected *Zantedeschia aethiopica* plants without induction, the level of polyphenols oxidase increased by 12 folds. The priming with methyl jasmonate also followed the same trend for peroxidase activity (Luzzatto-Knaan et al., 2014).

Genes expression following calla lily soft rot bacteria attack

Biochemical mechanisms of resistance against calla lily soft rot are coordinated by the expression genes. The expression of genes representing the induced system resistance pathway in *Zantedeschia* is species dependent. Basal levels of expression of aspartate aminotransferase, phenylalanine ammonia-lyase and lipoxygenase 2 (*lox2*) are higher in *Zantedeschia aethiopica* than in susceptible *Zantedeschia* hybrids (*Aestivae* section) (Guttman et al., 2021). The gene lipoxygenase 2 encodes a key enzyme involved in the biosynthesis of the defence signalling jasmonic acid. The gene aspartate aminotransferase acts as a regulator of carbon-nitrogen metabolism and amino acids synthesis during plant defence response to necrotrophic bacteria. The expression of the phenylalanine ammonia-lyase gene is the first step in the phenylpropanoid pathway (Guttman et al., 2021). This pathway leads to the synthesis of phenolic compounds. Its upregulation explains the observed accumulation of phenolic compounds around the infection site in the *Zantedeschia aethiopica* (Guttman et al., 2021). The expression of these genes markedly increases in *Zantedeschia aethiopica* after infection by *Pectobacterium carotovorum* strain PC16 and WPP14 (Khadka et al., 2020) and infection by *Pectobacterium brasiliense* (Guttman et al., 2021). Although the expression of these genes in susceptible hybrids cultivars was upregulated, their level of upregulation was lower than that of *Zantedeschia aethiopica* (Guttman et al., 2021). The behaviour of expression of the pathogenesis-related protein (*pr1*) which represents the systemic acquired resistance does not follow this trend. Its expression was downregulated in both *Zantedeschia*

aethiopica and the calla lily hybrid 'Captain Romance' infected by *Pectobacterium brasiliense* (Guttman et al., 2021) while it was upregulated when *Zantedeschia aethiopica* was infected by *Pectobacterium carotovorum* PC16 and WPP14 strains (Khadka et al., 2020). Data from these studies suggest that the level of expression of these genes depends greatly on the species of the bacteria or strain-inducing the disease.

Breeding for resistance against calla lily soft rot

As shown by research evidence described in previous sections, it is clear that *Zantedeschia* section calla lilies possess some levels of resistance against calla lily soft rot bacteria higher than those in the *Aestivae* section. However, this resistance cannot be transferred through classical breeding methods (Wei et al., 2017). The resultant hybrids suffer from Plastome genome incompatibility (PGI). Calla lily plants suffering from PGI are characterised by endosperm degeneration, abnormal embryo growth and disturbed plastid and nucleus (Wei et al., 2017). Tissues of plants suffering from PGI contain an incompatible plastome and have less chlorophyll content compared to a healthy one and this can be easily identified using the leaf colour. The plants affected by PGI are less vigorous than normal plants (Snijder et al., 2004b). Hence, plant genetic engineering can be considered as a way forward to address the issue of calla lily soft rot. The first aspect that can be considered is the transfer of genes of colour to *Zantedeschia* section cultivars. Calla lily cultivars in the *Zantedeschia* section have shown a higher level of resistance against calla lily soft rot, but they produce predominantly white flowers. Transferring genes of colour would improve their market value and become an alternative for calla lily hybrids which are susceptible to calla lily soft rot. Moreover, transferring genes of resistance to calla lily cultivars in the *Aestivae* group using genetic engineering techniques should be explored. A successful attempt has been previously made by transferring the ferredoxin-like protein gene to produce soft rot resistant calla lily. In this attempt, the *Agrobacterium tumefaciens* carrying the plasmid containing the plant ferredoxin-like protein gene was co-cultivated with shoot basal discs of *Zantedeschia elliotiana* Florex Gold'. Transgenic calla lily plants generated through this *Agrobacterium tumefaciens* mediated transformation were resistant to calla lily soft rot caused by *Pectobacterium carotovorum subsp. carotovorum* due to the overexpression of ferredoxin-like gene (Yip et al., 2007). Using X-ray mutagenesis on *Zantedeschia aethiopica* varieties, some new varieties with important commercial traits and resistance to *Pectobacterium brasiliense* were developed (Reznik et al., 2021). There are opportunities for further research in the area of genetic engineering for calla lily soft rot resistance/tolerance. The focus should focus on safe and accepted practices.

Conclusions

This review critically analysed the oldest and the most recently available information about calla lily soft rot disease. The scientific evidence gathered has shown that this disease is poly-aetiological. The disease is mostly manifested when factors favouring it prevail and virulence mechanisms are activated. Gathered evidence highlighted various practices that have been in use for the management of calla lily soft rot and the reasons for their inability to provide a sustainable solution against this disease. It has also shown that there are potential biocontrol methods that are being investigated which include the use of

microorganisms, plant extracts as well as phenolics and volatiles. The resistance to calla lily soft which is the focus of the current research is explained to be from ecological adaptations and biochemical mechanisms triggered by gene expression following the attack by calla lily soft rot-causing bacteria. For sustainable management of the disease, the use of genetic engineering is proposed for the development of resistant varieties with commercial traits.

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