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A Review

Microbial soft rot of cultivated fruits and vegetables

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ABSTRACT

The nutritional richness of fruits and vegetables makes them an ideal target for microorganisms, causing in particular soft rot. The microorganisms responsible for this pathology are generally found in the environment, and are endowed with a very important enzymological power, the main action of their pathogenicity. These enzymes, which allow the degradation of the plant cell wall, allow them to cross the protective wall of the plant, causing a liquefaction of tissues, whose environmental conditions as well as transport and storage conditions favour the development of these phytopathogens. A better understanding of spoilage microorganisms and the characteristics of spoilage should allow the development of new conservation and protection technologies and reduce the loss of vegetables due to spoilage. This review summarizes the main literature data on soft rot, and the diversity and mode of action of the main microbial causal agents.

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1. Introduction

Fruits and vegetables represent a very important nutritional source for humans, due to their richness in water, vitamins and micronutrients [1, 44]. They are part of the daily human diet, which it is recommended by World Health Organization (WHO), Food, and Agriculture Organization (FAO) to consume at least 400 g of fruits and vegetables per person per day. This consumption helps humans to combat nutrition-related chronic diseases [3, 1].

In addition, post-harvest diseases are a major cause of fruit deterioration and unprocessed vegetables [43]. Indeed, significant economic losses of fruits and vegetables can therefore result for farmers, the food industry and customers worldwide. Deterioration means any undesirable changes in organoleptic (color, flavor, odor…etc.), nutritional and sanitary quality, which can occur at any stage of the commercial chain (cultivation, transport or storage) [29, 38, 56]. Physicochemical (e.g. oxidation, post-harvest handling) and biological agents are responsible for this change, particularly those related to phytopathogenic microorganisms [44, 29].

Generally, this type of weathering is known by the term “rot”, some of which appears in soft form, which reduces the shelf life of fruits and vegetables [51, 26].

Moreover,microbial soft rot is the maincause of post-harvest loss of 20-25% of fruits and 30% of vegetables destined for consumption [1, 38]. This percentage is higher in countries during development because there is a lack of appropriate storage and transport conditions, not to mention climatic conditions which may be an influential parameter [1]. However, the main cause of soft rot in fruits and vegetables is the proliferation of bacteria, fungi, and sometimes yeasts [59]. These microorganisms use the nutrients (sugar, protein, lipid, and vitamins), found in the plant product in order to survive, and are known by the name SSO, which stands for Specific Spoilage Organism [56, 29]. However, some opportunistic germs can infect fruits and vegetables already damaged by other plant pathogenic microorganisms that have passed through the

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protective wall of the vegetables [38].

In addition, the pathogenicity of these microorganisms is mainly related to three factors: (1) their ability to grow in temperatures ranging from 5°C to 65°C [29], (2) the production of a wide range of enzymes called PCWDE (Plant Cell Wall Degrading Enzymes), which have the ability to degrade plant structures composed of: pectins, cellulose, hemicellulose and others**,** causing cell necrosis and tissue maceration [38]. Finally, (3) the production of toxins dangerous to human and animal health [38], as is the case of aflatoxin and ochratoxin, considered carcinogenic agents, produced mainly by the fungi *Aspergillus* and *Penicillium, which are* found in air, soil and water [5, 29].

Because of this contamination by toxins and mycotoxins, many fruits and vegetables that are part of the daily human diet have been added to the list of products exposed to mycotoxin contamination [8]. In addition, the classical evolution of microorganisms in perishable products such as fruits and vegetables are limited because the product is released for sale before control results are reported [56]. In addition, some fruits and vegetables contaminated mainly by bacteria show no change in appearance and texture, which causes many cases of intoxication [29].

It is from this perspective that the review presented summarizes the main findings on the microorganisms responsible for the soft rot of fruits and vegetables.

2. General information

2.1. Definition

Soft rot is the most diagnosed pathology affecting cultivated plants. It is most often caused by microorganisms, such as: *Erwinia* and *Penicillium,* or by agents related to the environment (insects, irrigation water ...etc) [15, 38, 35].

This pathology is characterized by a symptomatology visible or invisible to the naked eye, during harvesting and post-harvest or during storage of harvested fruits and vegetables [39, 33]. It is the result of the action of a set of enzymes called Plant Cell-Wall Degrading Enzymes or PCWDEs (Plant Cell-Wall Degrading Enzymes), which render the fruit or vegetable unfit for consumption [13, 38].

2.2. Symptoms

Soft rot as already described, microorganisms are the main cause of it, which act on several parts of the host plant, namely: pale green or yellowish leaves and stunting of the plant, which occurs during the storage of fruits and vegetables especially in places with high humidity [25]. Symptoms appear on fruits and vegetables (fig 1) according to two stages:

Stage 1: Symptoms are manifested by the presence of spots, which may also present as necrosis, brown with a black spot in the center, or brown to black lesions at the end of the fruit stem, rapid spread can be observed throughout the whole fruit causing: pitting, sticky spots and decomposition of the entire tissue, which becomes spongy with the change in color from white to creamy brown [36, 24, 33].

Stage 2: Decayed tissue develops an unpleasant odour and becomes viscous as the microorganism cause the formation of a mucous suspension with a foul odor [7].

The same principle is exposed to fruits and vegetables during storage and transport depending on climatic influences, or in the case of mixed infection [19].

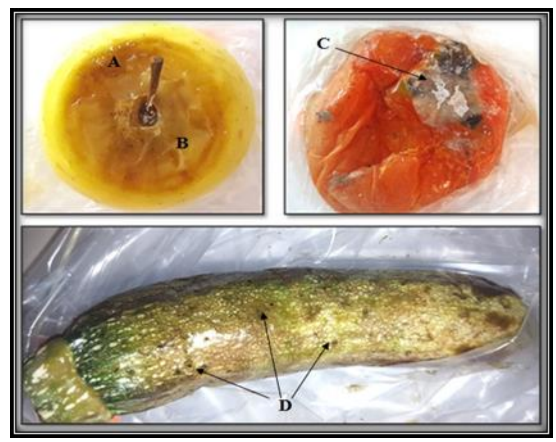

Fig 1.Photograph of soft rot symptoms (A- Color change [yellowtobrown]; B- Tissue liquefaction, C- Infection sites: viscous; D- Brown necroses with a dark black dot).

2.3. Factors influencing

Microbial soft rot is a result of interaction between different factors (Fig 2) and pathogenic or contaminating microorganisms [28].

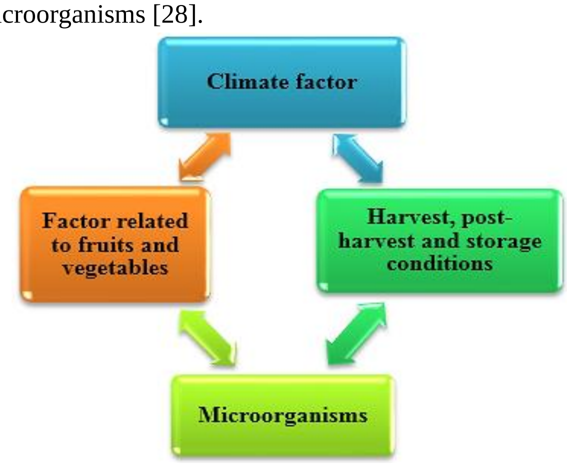

Fig 2. Diagram of the interaction between the different factors that influence the development of soft rot.

2.4. Environmental factors

2.4.1. Climatic factors

The variation in temperature and humidity from one region to another in the transport of fruits and vegetables has a direct effect the growth and development of pathogenic microorganisms on the surface of plants (fruits and vegetables) [18, 2].In addition, exposure to light in the field and high humidity in greenhouses promote rapid disease development, causing crop losses [36, 18].

2.4.2. Harvest, post-harvest and storage conditions

Harvest and post-harvest conditions have a direct effect on the development of soft rot, as good or poor handling practices during this period provide fruit and vegetables with shelter from cracks that make them vulnerable to pathogens [18, 2, 54]. However, hygiene's level and temperature stability during the storage and marketing period may or may not protect fruits and vegetables from soft rot microorganisms [2, 6].

2.5. Factors related to fruits and vegetables

Fruits and vegetables represent a food source and an environment rich in nutrients, vitamins and water, which makes them susceptible to microorganisms, especially pathogens [28, 18]. In addition, the variation in the pH spectrum means that a wide range of pathogens (yeast, mold, bacteria) can live and infect fruits and vegetables [18].

2.6. Microorganisms

Some fruits and vegetables harbour spoilage microorganisms, and the onset of symptoms is associated with two factors: on the one hand, the microbial production of enzymes that degrade the cell wall, especially pectinases that degrade pectin polymers. As a result, fruits and vegetables become more susceptible to the effects of the microorganisms responsible for soft rot [20]. On the other hand, the complex interaction between the virulent factors of the phytopathogenic germs and the defense mechanisms of plant tissues allow the pathology to appear [18].

3. Development cycle

The skin of fruits and vegetables forms a barrier against the penetration of germs that spoil them, and this extends their shelf life after harvest [18]. In fact, resistance to microbial invasion is very strong when the plant product is still attached to the plant, but it decreases during harvesting or ripening, and during storage or display for sale. Thus, fruits and vegetables will be damaged by saprophytic flora [58]. However, there are asymptomatic infections, such as the infection of mango branches by Dothiorelle dominicana, which are revealed only after harvest and during marketing [55]. Moreover the degree of infection can range from a simple alteration of the external appearance to partial or total pulp rot [10], as already presented in Figure 1.

Generally, soft rot occurs in infected fruits and vegetables in the following stages (Fig 3):

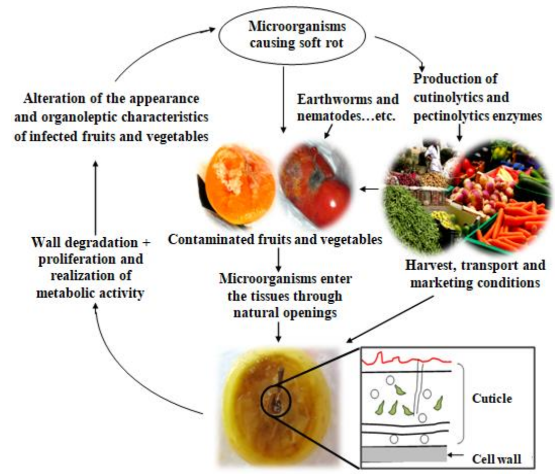

Fig 3. Diagram of the development cycle of microbial soft rot in fresh fruits and vegetables.

- ✓ *Entry of microorganisms:* the spoilage process is triggered by the penetration of the germs responsible for the disease through the end of the stem, which is the main site of infection due to the wound caused by harvesting operations, or by using the structure and composition of the surface of fruits and vegetables (stomata, scars, etc.), which represent entry routes. However, some germs are able to cross the cuticle of vegetables by penetrating damaged tissues because of their virulence factors (production of cutinolytic, pectinolytic enzymes, etc.) [18, 45];

- ✓ *Proliferation of microorganisms and modification of organoleptic quality:* the nutrients existing in fruits and vegetables facilitate the growth and multiplication of the germs responsible for soft rot and lead to visual changes: musty smell, decrease in color intensity by enzymatic hydrolysis of the pigments, viscous or sticky appearance, softening of fruits and vegetables due to pectinolytic activity, etc [29, 56].

4. Plant selectivity towards microorganisms

The composition of fruits and vegetables is similar for some elements and different for others, this difference makes them targeted by some microorganisms compared to others:

- Yeasts and fungi most often infect the fruit, because they are low in acidity, and this favours the growth of fungi; as a result, the fruit will be damaged, and rotten;
- Bacteria infect vegetables because they are less acidic than fruits, causing their rotting [29, 1].

For example, spinach is rotten most often in hot, humid conditions, due to bacteria that feed on the nitrates with which it is rich. In contrast, strawberries rot quickly after harvest, since cutinolytic microorganisms [37, 23] infect them.

5. Microorganisms involved

Different types of microorganisms can cause soft rot; their nature depends on growing conditions, shelf life of fruits and vegetables, etc [44].

5.1. Bacteria

There is a wide variety of phytopathogenic bacteria that can penetrate the protective coating of fruits and vegetables and cause soft rot. The main types include:*Pectobacterium, Pantoa*, *Dikeya* and *Brenneria* [30] are facultative anaerobic Gram-negative bacteria, which are part of the Enterobacteriaceae family. These genera are capable of oxidizing D-glucose to various forms of gluconate, and produce extracellular pectinase enzymes, and cause disease, but only when host resistance is impaired, and this infection is temperature dependent in commercial stocks [47, 30].

For example, the species *Pectebacterium carotovorum* is the most common in rhizosphere-associated soft rot: in roots, bulbs and tubers (potato, onion) (Fig 4, B, C and D), and in peppers [17, 16].

5.1.1. Genus Erwinia

Members of the genus Erwinia are mainly opportunistic pectinolytic phytopathogenic bacteria (Fig 4, A) [9].

The analysis of rDNA makes it possible to split some members into other genera: Enterobacter, Thus, the species Erwinia chryasanthemii is commonly found in the soil. The transition between the saprophytic and pathogenic lifestyles is determined by a regulated response of virulence factors, under favourable environmental conditions resulting in endopectin lyase activity [27]. It is responsible for the degradation of potato (*Solanum tuberosum*) seed wall before or during the germinative phase, causing delayed emergence [32].

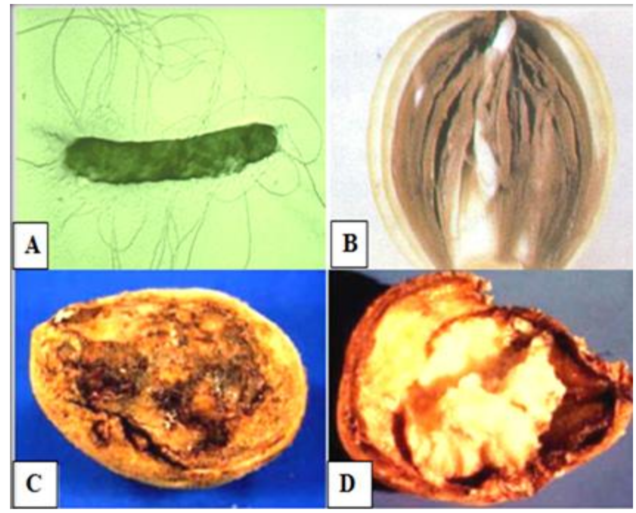

Fig 4. Microscopic observation of Erwinia and the appearance of soft rot in some vegetables (A- Electronic microscope observation of Erwinia shows a peritrichous flagellum; B- Aspect of bacterial soft rot in onion; C and D- Appearance of soft rot symptoms in the exterior and interior of potato tubers caused by Pectebacterium spp bacteria [9, 11, 12].

5.1.2. Genus Pseudomonas

This genus groups together Gram-negative psychotrophic pectinolytic bacteria belonging to the *Pseudomonaceae* family, whose presence indicates the beginning of deterioration [35]. *Pseudomonasaeroginosa* and *Pseudomonas fluorescens* are the most important species in carrot and tomato soft rot [49].

5.1.3. Other bacteria

There are other bacteria involved in decay, such as [34]:

- *Leuconostoc mesenteroide*: mesophilicand psycrotrophic lactic acid bacterium, which is usually found in small quantities on the plant surface, but can proliferate during storage of carrots and tomatoes ;
- The pectinolytic bacteria *Serracialiquefaciens*and *Vibrio anguillarum* which can cause this disease, also the species *Bacillus subtilis, Bacillus cereus*, *Clostridiumperfringens* and *Staphylococusxylosus,* which cause soft rot in: tomatoes and some fruits and vegetables during storage.

5.2. Yeasts and fungi

Yeasts and fungi are inferior fungi, most often responsible for post-harvest soft rot [39]. There is a wide range of these phytopathogens, the most important of which are the following:

5.2.1. Yeasts

5.2.1.1. Geotrichum candidum

G. candidum is a yeast fungus, the causative agent of soft rot in tomatoes, potatoes and other fruits and vegetables [31]. It is most found in the soil, and causes tuber soft rot in flooded soil. This yeast has optimal growth in the temperature 25 °C and pH 5 to 5.5, in the presence of oxygen in a medium very rich in carbon sources (D-glucose, D-galactose, ...etc) [57].

5.2.1.2. Candida spp

Candida spp are opportunistic yeasts and plant parasites, which are characterized by cream to yellowish colonies, also, they are able to ferment sugars, and use alcohol and peptone as a source of carbon, causing soft rot of pineapples and other fruits and vegetables, of which the most pathogenic species are: *C. krusei,C. guilliermondii* and *C. albicans* [42, 60, 48].

5.2.1.3. Other yeasts

There are several types of yeasts that cause fruit and vegetables to rot, before or after harvest, we will mention among others:

- *Verticilum theobromae* that infects bananas [21];
- *Debaryomyces hansenii*, *Pichia polymorpha*, *Pichia Kuriavzevii* and*Torulopsis*, *hansenula* which causefruit deterioration**,** plus, *Trichodermaherzianum*, which ferment sugars intoalcohols; which gives a bad taste and odor in infected tubers during storage [50];
- *Saccharomyces exiguns* or *Saccharomyces italicus* that infectsmangoes [52].

5.2.2. Fungi

Moulds infect fruits and vegetables in two stages of the production chain: in cultivation (fields) and in storage [39], causing the deterioration of plant products, of which the following are the most pathogenic:

5.2.2.1. Fungi of the field

5.2.2.1.1. Genus Alternaria

Species of this genus are ubiquitous fungi in the environment, saprophytes, and very abundant in the atmosphere, with growth temperatures between 5 and 30 °C [46]. They generally colonize tubers infected with dry mold, causing their rots in the harvest and post-harvest, especially tomatoes, citrus fruits (tangerine, orange, lemon), melon and apple. The most pathogenic species in this genus are:*Alternaria alternata* and *Alternaria solani*, which produce a greyand black rot [39].

5.2.2.1.2. Genus Fusarium

Species of this genus are ubiquitous and opportunistic plant pathogens of plants and agricultural products, or saprophytes on cellulotic plant debris and matter, of which the most pathogenic species is *Fusarium oxysporum,* which causes rot ofbotanical families: *Solanaceae* (tomato) and *cucurbitaceae* (zucchini), ...etc [39].

5.2.2.2. Storage fungi

5.2.2.2.1. Genus Penicillium

It is the most diverse genus, with somespecies representing the main cause of agricultural loss of fruits and vegetables after harvest, storage and warehousing [39]. Species in this genus are characterized by a branched mycelium, which causes soft rot with the production of mycotoxins, the most pathogenic of which is: *Penicilliumexpansum,* which infects apples, pearsand citrus fruits [14, 41].

5.2.2.2.2. Genus Aspergillus

It is a ubiquitous plant pathogen, saprophyte that colonizes plant debris and deteriorated plant products in tropical and subtropical areas [39]. It produces dangerous mycotoxins, the most important of which is patulin, which accumulates in plant tissues and induces their deterioration [41]. The most pathogenic species are: *Aspergillus oryzaethat infects* oranges, and *Aspergillus niger* that infects apples [4].

5.2.2.2.3. Other fungi

There are other types of molds that cause soft rot in fruits especially, such as *Botrytis cinerea*. This species infectsstrawberries, kiwi fruit, grapes and other fruits and vegetables, giving a gray mold on the surface of rotten fruit [41].

6. Pathogenicity and physiopathology

The pathogenicity of these microorganisms is due to their ability to produce different compounds during host cell invasion; these compounds are called virulence factors**,** which cause adverse effects on host fruits and vegetables and may present a health hazard to the human consumer [27, 38, 53, 49].

6.1 The production of PCWDE enzymes (Plant Cell Wall Degrading Enzymes)

It is a wide range of enzymes secreted by most pectinolytic saprophytic bacteria, as well as phytopathogenic yeasts and molds [38].

Because of plant-microorganism interactions (fig 5), microbial deterioration is reflected in a first place by the renewal of low molecular weight compounds (amino acids and other compounds containing nitrogen and sugar), which generate an unpleasant odor, or in a second place the degradation of polymers, such as proteins or pectins following the action of certain enzymes [49, 27, 50]. These enzymes allow pathogens to easily invade living plants, causing disease with a high degree of metabolic plasticity [49].

The strains whom produce the most PCWDE cause deterioration on different plants, pectinase is the most important one, notably pectate lyase through the degradation of pectin which is responsible for the reorganization of the wall by transforming polygalacturonic acid into oligogalacturonic acid [49]. For example, in *Erwinia chrysanthemi* and *Penicillium digitatum*, the enzymescellulase, xylanase, pectin methylesterases, lyases, proteases, and phospholipase have a role in pathogenicity and are capable of macerating plant tissues and disclosing disease symptoms [27].

6.1.1. Pectin degradation

This process involved the depolymerization of pectins in the cell wall composed of D-galacturonate residues and certain rhamnose molecules. There are several types of pectinases, which perform different functions: endopectinases cut the different functions: endopectinases cut the give a mixture of oligomers, exopectinases attack the reducing end of the polymer and produce dimmers. The following enzymes are among the best known [27]:

-Pectate lyase: plays a major role in the symptoms of soft rot through the production of the 4-5 unsaturated oligomer tip;

-Pectin metheyleestirase: facilitates the action of pectate lyase by eliminating the methoxyl groups of pectin (source of carbon);

-Pectin lyase: causes the softening of tissues resulting from the degradation of vegetable pectin and degenerates a viscous mass.

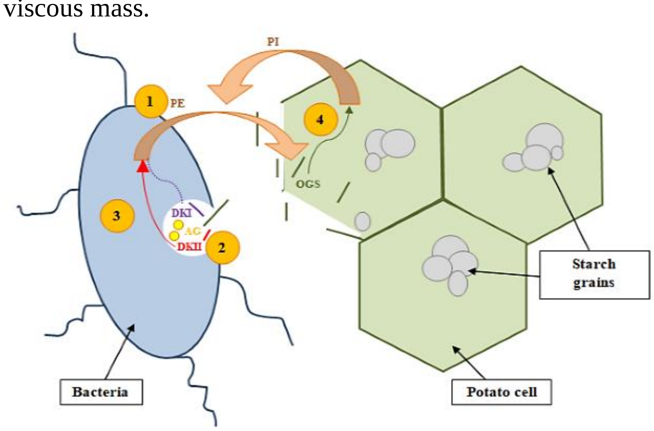

Fig 5. Schematic representation of the mechanisms involved in the attack of potato tissues by Dickeya spp (1. Bacteria synthesizes the pectinolytic enzymes (PE), including pectate lyase and polygalacturonase which catalyze the depolymerization of wall pectin into oligogalacturonates (OGS); 2. The (OGS) are absorbed by the bacteria and degraded to 5-Keto-4deoxyuronate (DKI), 2-5-diketo-deoxy-gluconate (DKII) and galacturonic acid (AG) under action of oligo-galactoronide lyase ; 3. the (DKI) and (DKII) and other compounds as a result of degradation increases the production of PE and increases the virulence of the bacteria; 4. The (OGS) to induce resistance mechanisms in the plant against these attacks such as the production of protease inhibitors (PI) [22].

In addition, plant cells usually suffer from a high osmotic water potential, due to the localization of intracellular bacteria beyond the phelloderm layer of tubers, which affects turgidity [47]; other components are also degraded under the action of microbial enzymes [38, 50]:

- Starch and sugar are metabolized to maltose by amylase, plus unpleasant odors and flavors develop with lactic acid and ethanol;
- Proteins and proteinaceous material are broken down into polypeptides and amino acids;
- Many pathogens have lipolytic activity (via lipase) to degrade the lipids that make up plants.

6.2 Lipopolysaccharides (LPS)

The external wall composition of Gram-negative bacteria (LPS) inhibits the hypersensitivity (HR) reaction in the plant and provides resistance against host- produced antimicrobial substances [47].

6.3. Bacteria communication system

Many bacteria use a "quorum-sensing" cell-to-cell communication system to regulate the expression of pathogenicity genes involved in deterioration (production of enzymes to destroy surrounding tissue, biofilm formation) [38].

6.4. Production of toxins

In host plants, pathogenic filamentous fungi can synthesize toxic secondary metabolites in plant tissues [39]. The synthesis of these toxins isgenerally triggered after harvest and during storage of harvested fruits and vegetables, since conditions will be favourable for the growth of phytopathogenic moulds, the most important of which are the producer moulds [41, 40]:

- *Fusarium*: synthesizes six types,which are : Fumonisins, Trichothecenes, Zearalenones, Moniliformin, Beauvericin and Fusaproliferin;

-*Alternaria*: synthesizes altermaricacid, alternarioles and altertoxins ;
- *Aspergillus*: synthesizes aflatoxinand ochratoxin;
- *Penicillium*: synthesizes ochratoxins,citrimin and patulin.

Phytopathogenic microorganisms are not only involved in the deterioration of fruits and vegetables, but they can also represent a serious danger to human health. Thus, the presence of pathogens on fruits and vegetables can cause food poisoning, or even cause mycotoxycosis in humans following ingestion of mycotoxins synthesized and contained in fruits and vegetables infected with toxiconogenicmoulds [18, 5].

7. Conclusion

The microorganisms responsible for the soft rot of fruits and vegetables represent a category of phytopathogens that are very dangerous, and this is due to their ability to produce a wide range of enzymes called PCWDE, the most important of which is pectinase. This enzyme allows so-called pectinolytic microorganisms to cross the protective barrier of fruits and vegetables, thus causing soft rot.Thisis why it is necessary to adapt means of fighting these microorganisms, by using chlorinated solutions, or even by inoculating resistance genes in host plants.

Conflict of Interest

The authors declare that they have no conflict of interest

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