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REVIEW

Green solutions and new technologies for sustainable management of fungus and oomycete diseases in the citrus fruit supply chain

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Abstract

This review deals with major diseases caused by fungi and oomycetes in the citrus supply chain, including post-harvest fruit diseases, and summarizes the strategies and techniques that may be adopted to prevent the damages and losses they cause. Its scope is to highlight the contribute that smart technologies provide towards new solutions for sustainable and safe management strategies of these diseases. Particular attention is given to the application of biopesticides, natural substances, resistance inducers and biostimulants to prevent fruit rots. The review focuses also on mycotoxins and mycotoxigenic fungi that contaminate fresh fruit and food products derived from citrus fruit, an aspect that has been little investigated and regulated so far. An additional relevant aspect addressed by the review is the early detection and routine diagnosis of fungal and oomycete pathogens that threat the international trade and long-distance shipment of citrus fruit, with a particular emphasis on quarantine pathogens. In this respect, the opportunities offered by new practical, rapid, sensitive and robust molecular diagnostic methods are briefly discussed.

Keywords Biopesticides · Biological control agents · Molecular diagnostics · Forecasting models · RPA · Mycotoxins · Quarantine pathogens · *Alternaria* · *Colletotrichum* · *Phyllosticta citricarpa* · *Phytophthora* · *Penicillium* · *Plenodomus tracheiphilus*

Introduction

Citrus, the most important cash fruit crop worldwide (Ismail and Zhang 2004), includes plant species belonging to the genera *Citrus*, *Eremocitrus*, *Fortunella*, *Microcitrus* and *Poncirus*, native to South, East and Southeast Asia, Melanesia and Australia, (Khanchouch et al. 2017; Wu et al. 2018).

At a global scale, citrus are cultivated in more than 140 countries (FAO 2020). Citrus fruits are mostly intended for human consumption, as fresh fruit and/or derived beverages (Talibi et al. 2014). The international production of citrus fruits encompasses mainly sweet oranges (65%), mandarins (19%), lemons and limes (11%), and grapefruits (5%) (FAO 2020). In this respect, countries from the Mediterranean area are the main fresh fruit producers for the international market worldwide (Khanchouch et al. 2017).

A major constraint to the successful trade of citrus, both domestically and internationally, is the occurrence of severe diseases affecting plants and/or fruits throughout the entire supply chain (Agosteo et al. 2013; Liu et al. 2013; Naqvi 2006; Talibi et al. 2014). In this respect, citrus are susceptible to infection by numerous fungal and oomycete pathogens, from the nursery to the fruit bearing stages, resulting in yield losses ranging on average between 30 and 50% (Chalupowicz et al. 2020; Strano et al. 2022). Diseases of plants such as the Mal Secco caused by *Plenodomus tracheiphilus*

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and the Foot and Crown Rot, Root rot and Brown Rot of fruit disease complex caused by *Phytophthora* species are among the major limiting factors to citrus cultivation in the Mediterranean basin area (Cacciola and Magnano di San Lio 2008; Migheli et al. 2009). Additionally, due to their high-water content, nutrient composition and acid pH, citrus fruits are highly susceptible to infection by various fungi and oomycetes (Tripathi and Dubey 2004). Fruit infection occurs in both the pre-harvest (from bloom to harvesting stage) and postharvest (picking, packaging, storage, transportation and shelf life) stages (Naqvi 2006). The most common pre-harvest pathogens cause significant reductions in both fruit yield and quality and comprise species in the following list. At least, 24 *Colletotrichum* species, including the prevalent species *C. gloeosporioides* and *C. karsti*; the tangerine pathotype of *Alternaria alternata*; *Phyllosticta citricarpa*, a major citrus quarantine pathogen for the Mediterranean and European region; the frequently isolated *Phytophthora* species, such as *P. nicotianae*, *P. citrophthora* and *P. palmivora*; the less frequent *P. hibernalis*, *P. syringae* and *P. mekongensis* (Cacciola and Magnano di San Lio 2008; Crous et al. 2017; Gai et al. 2021; Guarnaccia et al. 2017; Khanchouch et al. 2017; Naqvi 2006; Puglisi et al. 2017; Wang et al. 2021). Pre-harvest infections can also manifest themselves during the postharvest stages, in addition and notwithstanding the concomitant attacks of typical postharvest wound-dependent fungi, like *Penicillium digitatum*, *P. italicum* and *Geotricum candidum* var. *citri-aurantii*, which, together, are the causative agents of the most destructive postharvest rots affecting citrus fruits worldwide (Bhatta 2022; Ferraz et al. 2016; Kanashiro et al. 2020; Palmieri et al. 2022; Palou 2014; Talibi et al. 2014).

Nowadays, the management of plant diseases dictates the adoption of smart strategies in line with the needs and the demands of society, regarding the availability of products of good quality and, at the same time, toxicologically and environmentally safe.

The purpose of this review is to provide a current picture of the implications of outbreaks of plant diseases caused by fungi and oomycetes in the citrus supply chain, highlighting the state of art and new promising improvements available thanks to the development of smart management strategies. The review will first introduce the main fungal and oomycete plant pathogens and the disease they cause and then it will summarize the knowledge about specific management options, with particular emphasis on novel ecofriendly tools and sustainable disease management strategies, including the management of contamination of food products by mycotoxins. New, rapid, accurate and cost-effective molecular techniques for the early detection of fungal and oomycete citrus pathogens will be also discussed, because we believe they are a necessary component of any sustainable and integrated citrus disease management strategy.

Fungal and oomycete diseases affecting citrus plants

Mal Secco caused by *Plenodomus tracheiphilus*

The mitosporic fungus *Plenodomus tracheiphilus* (formerly, *Phoma tracheiphila*) is a quarantine plant pathogen causing the disease known as Mal Secco (De Gruyter et al. 2013; EPPO 2015). The disease was named after the Italian words male (disease) and secco (dry) (Migheli et al. 2009; Nigro et al. 2011). The term Mal Secco refers to nonspecific symptoms and was initially used in a broad sense to indicate citrus diseases of various origins (Migheli et al. 2009). Later, Petri used the term Mal Secco of citrus in a stricter sense to indicate a tracheomycosis widespread in lemon orchards in Sicily (Migheli et al. 2009).

The principal host of *P. tracheiphilus* is lemon (*Citrus limon*), although the disease can be found on other citrus, including citron (*C. medica*), bergamot (*C. bergamia*), lime (*C. aurantifolia*), sour orange (*C. aurantium*), and rough lemon (*C. jambhiri*) (Nigro et al. 2015). The European and Mediterranean Plant Protection Organization (EPPO) included this pathogen in the A2 list recommended for regulation as quarantine pests. Moreover, *Plenodomus tracheiphilus* is also in a list of pests recommended as non-regulated non-quarantine pests (RNQPs) in the EPPO region (Picard et al. 2018) and is considered of quarantine concern by several regional plant protection services worldwide (Asia and Pacific Plant Protection Commission—APPPC, Caribbean Plant Protection Commission—CPPC, Comité Regional de Sanidad Vegetal para el Cono Sur—COSAVE, European and Mediterranean Plant Protection Organization—EPPO and North American Plant Protection Organization—NAPPO) (EPPO 2015; Migheli et al. 2009; Nigro et al. 2011; Zhao et al. 2021).

The typical lemon rootstocks that stand out for their high susceptibility are: (i) sour orange (*C.* × *aurantium*), the most widespread lemon rootstock in Italy, Greece, and Turkey; rough lemon (*C. jambiri*); the (ii) volkamer lemon (*C. volkameriana*) and the (iii) alemow (*C. macrophilla*) (Migheli et al. 2009). Conversely, other rootstocks, such as Cleopatra mandarin (*C. reshni*), trifoliate orange (*Poncirus trifoliata*), and citranges (*C.* × *sinensis* × *P. trifoliata*) have been reported as being less susceptible (Migheli et al. 2009). There is evidence that the rootstock influences the susceptibility to Mal Secco of the scion (Migheli et al. 2009; Solel and Spiegel-Roy 1978).

The Mal Secco disease induces a broad array of specific and non-specific symptoms that can occur independently or jointly in the manifestation of the disease (Migheli et al. 2009) (Fig. 1).

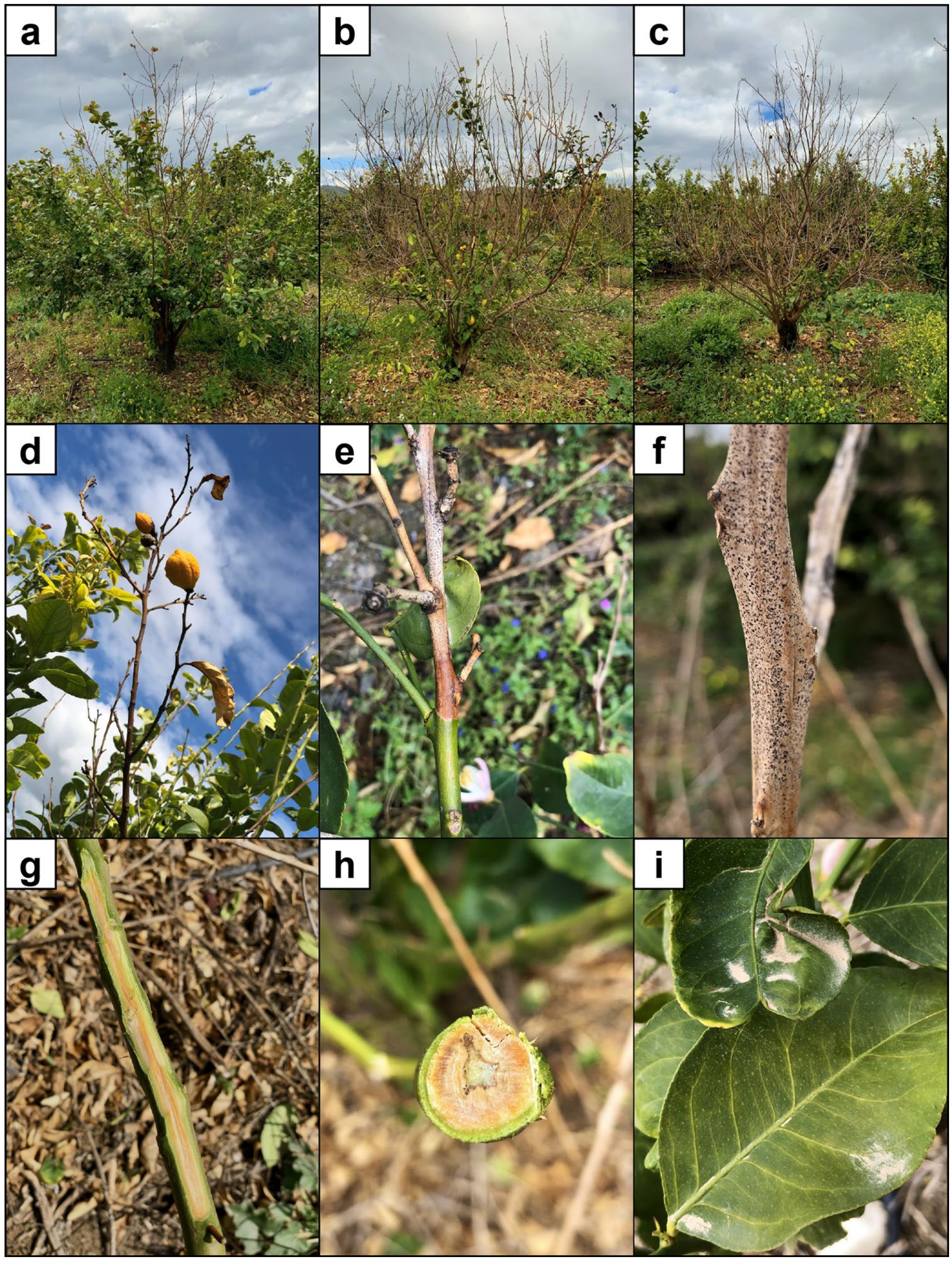

Fig. 1 **a**, **b** and **c**, progression (from left to right) of the severity of wilting and defoliations of twigs in a young lemon tree affected by Mal Secco in a commercial orchard in Sicily (Italy); **d** and **e**, shedding of leaves and defoliation of apical twigs; **f** withered twig of lemon with scattered pycnidia of *Plenodomus tracheiphilus*; longitudinal (**g**) and transverse (**h**) sections on a lemon twig with the typical orange-reddish discoloration of the wood; **i**, clearing and chlorosis of leaf veins in a lemon tree affected by Mal Secco

Early symptoms usually appear on the leaves of the uppermost shoots, which display a slight discoloration of the primary and the secondary veins (Fig. 1i). As the disease progresses, the leaves lose their shine, turn yellow, wither and fall down, mostly without the petioles, which persist on the shoots. The shoots often appear chlorotic on the apical part while maintaining a normal green color in the basal part (Fig. 1d, e), although sometimes they may turn brown. Newly infected shoots are characterized by a yellow or pink-salmon to reddish discoloration of the wood, which occurs also in the wood of the main and secondary branches as well as in the trunk, where the pathogen growth is progressing (Fig. 1g, h). With time, the plant undergoes a progressive basipetal desiccation of shoots, branches, and trunk, which leads to death of the whole plant (Fig. 1a–c) (Abbate et al. 2019; Migheli et al. 2009; Nigro et al. 2011; Russo et al. 2020).

When the pathogen infects the outermost woody rings of large branches, symptoms may only affect a portion of the host and less frequently the entire plant. Conversely, when infection starts in the main roots, symptoms can progress rapidly and plant death ensues in a short time: this is a variant of the disease known as Mal Fulminante (sudden death) (Migheli et al. 2009; Nigro et al. 2011). However, when infection starts from rootlets, as it frequently happens in young nursery plants and in bearing trees in groves, *P.*

tracheiphilus can remain segregated in the inner wood layers for several years. When the disease is compartmentalized in the inner wood layers, symptoms progress very slowly (Nigro et al. 2011). Nonetheless, once the pathogen reaches the external woody rings, the disease progresses rapidly, and the plant shows symptoms similar to those produced by Mal Fulminante (Nigro et al. 2011). The withering young shoots and main branches show a browning of the innermost woody cylinder and the discoloration of the wood progressively darkens until it acquires a blackish hue carrying a smell of overripe melon. This variant of the disease is named Mal Nero (black disease) (Nigro et al. 2011).

The two syndromes, namely Mal Fulminante and Mal Nero, do not affect only susceptible hosts, but can also occur in *Citrus* species known as tolerant, especially if they are grafted onto susceptible rootstocks (Nigro et al. 2011).

An additional specific trait of the Mal Secco disease is the presence of signs of the pathogen (Gentile et al. 2000; Migheli et al. 2009) such as small, black and globose pycnidia, produced starting at the end of the autumn, normally in 1- to 2- year-old slowly desiccating shoots or suckers. Their presence elicits the detachment of the epidermis from the underneath tissues, which is followed by penetration of air, resulting in the appearance of long silver-gray stripes on the affected plant parts (Nigro et al. 2011). The cracking of the epidermis makes it possible to observe pycnidia as black spots directly by the naked eye or with a low magnification lens (Nigro et al. 2011).

Overall, the evolution of the disease is strictly dependent on climatic conditions and host susceptibility. It is known that warm moist conditions lead to infection and disease development. It has been observed that the optimum temperature for the development of the disease ranges from 20 to 25 °C; therefore, the disease progression is more rapid in spring and autumn (Migheli et al. 2009). Temperatures above 30 °C inhibit mycelial growth and disease progression, but do not kill the pathogen within the infected tissues (EFSA 2014a; Perrotta and Graniti 1988). In addition to a suitable temperature, wind, hail and heavy rains contribute to *P. tracheiphilus* infections by causing wounds through which the pathogen can enter the host plant. Moreover, rain and wind are the main natural dispersal agents of the Mal Secco fungus (Krasnov et al. 2022; Migheli et al. 2009). In the lemon producing Mediterranean areas, the infection period depends on local climatic and seasonal conditions. In Sicily, Italy, infections usually occur from September to April (EFSA 2014a; Somma and Scarito 1986). Mid-November to mid-April was indicated as the most conducive period for Mal Secco infection in Israel, coinciding with the rainy season (Krasnov et al. 2022).

Statistical models based on climatic variables are increasingly being used as technical support for the development of sustainable control of plant pathogens in modern agriculture (Hasanaliyeva et al. 2022; Scortichini 2022). They may be useful as forecasting and decision-making tools (González-Dominguez et al. 2023; Rossi et al. 2012). A recent model using Maximum Entropy (MaxEnt) was recently applied to predict the geographic distribution of Mal Secco disease under current and future climatic scenarios (Krasnov et al. 2022). The two climatic variables that mostly contributed to forecast the distribution of this citrus disease were precipitation during the wettest month and minimum temperature during the coldest month. According to the MaxEnt model, although climate change is likely to reduce the overall extent of suitable areas for Mal Secco up to 23% by the year 2070, no shift of disease range is expected to occur in the Mediterranean basin. Mathematical models were also used to assess the spatial distribution pattern and dynamics of Mal Secco in lemon orchards in Israel (Ben-Hamo et al. 2020; Krasnov et al. 2022). Results of these studies indicated the rate of disease spread depends primarily on orchard management practices, such as the planting and irrigation systems, and cultivar susceptibility. In our experience, the phytosanitary status of both propagation material and nursery plants is a crucial aspect determining the incidence and severity of the disease in new lemon plantings.

To date, no single method is effective in controlling the Mal Secco of citrus. Common strategies of control are based on the application of improved agronomical practices including the reduction of fungal inoculum by pruning symptomatic twigs and branches, particularly withered shoots bearing pycnidia, and the timely removal of rootstock suckers. Spraying with authorized copper-based fungicides are also carried out, especially on young plants from nurseries (Abbate et al. 2019). However, these treatments are causing concerns related to the long-lasting persistence of copper in the environment with the consequent toxic effects toward plants, animals and soil microbiota, and related to the contamination of food (Abbate et al. 2019; El Boumlasy et al. 2022). In this respect, a new promising super absorbent polymer (SAP) has been shown to act as an efficient reservoir for the controlled release of copper, specifically in the treatment of pruning cuts of lemon twigs affected by the Mal Secco. The use of this SAP has resulted in longer windows of treatment and in a reduction of heavy metals dispersion in the environment (El Boumlasy et al. 2022).

Promising and environmentally safe strategies for the management of Mal Secco have been pursued through lemon breeding (Migheli et al. 2009) based on the selection of spontaneous lemon genotypes tolerant to infection. Accordingly, in the Ionian coast of Sicily (Italy), the traditional variety 'Femminello' has been in the past replaced with the cultivars 'Monachello' and 'Interdonato', two spontaneous hybrids between lemon and citron. The former cultivar is resistant but produces qualitatively lower and reduced fruit yield (Catalano et al. 2021; Migheli et al. 2009), while the latter produces high quality fruit but, differently from other more productive lemon cultivars, does not bloom several times during the year. 'Continella M84' and 'Femminello Zagara Bianca M79' are noteworthy Mal Secco-tolerant lemon selections. These two cultivars produce high-quality fruits but are less tolerant than 'Monachello' to *P. tracheiphilus* infections. 'Femminello Zagara Bianca M79' is having a certain diffusion in new commercial plantings due to the recrudescence of the disease in typical lemon-growing areas of Sicily (Cacciola and Gullino 2019). Among foreign lemon cultivars, only 'Meyer lemon' shows levels of resistance comparable to those of 'Monachello' and 'Interdonato', but its yield is unsatisfactory in terms of fruit commercial value (Migheli et al. 2009). Conversely, the early ripening and seedless triploid lemon-like hybrid, 'Lemox'®, initially patented as a Mal Secco-tolerant cultivar, proved to be as susceptible as 'Femminello Siracusano 2Kr', a mutant clone obtained by cobalt γ-radiation, known for its high yield potential, but very susceptible to the disease (Cacciola et al. 2010; Migheli et al. 2009; Russo et al. 2020).

Other interesting strategies for the selection of Mal Secco resistant/tolerant genotypes have been provided by the application of biotechnologies such as *in vitro* selection, somatic hybridization, and genetic transformation. *In vitro* selection involves culturing protoplasts and embryogenic calli in the presence of phytotoxic metabolites produced by the pathogen to identify toxin-tolerant lines. Somatic hybridization involves fusing protoplasts from different citrus plants to obtain interspecific, Mal Secco tolerant-genotypes. Genetic transformation mediated by *Agrobacterium tumefaciens* has led to the creation of transgenic clones of lemon with enhanced tolerance to Mal Secco. The studies related to these strategies, as well as the Mal Secco tolerant/resistant genotypes identified, are summarized in Table 1.

Currently, a new approach is being pursued in an ongoing breeding program of lemon for Mal Secco-resistance. The availability of a reference genome sequence of lemon 'Femminello Siracusano' (Di Guardo et al. 2021) and of segregating progenies obtained from crosses between resistant and susceptible lemon cultivars, facilitates the identification and mapping of Quantitative Trait Loci (QTLs), a prerequisite for marker-assisted selection (Catalano et al. 2021; Iwata et al. 2016). This strategy has been widely applied in breeding programs for resistance to other devastating diseases of herbaceous and tree crops, including citrus, such as Fusarium Head Blight and Stem Rust of wheat, Apple Scab and Citrus Huanglongbing, just to cite a few (Haile et al. 2019; Huang et al. 2018; Karelov et al. 2022; Liebhard et al. 2003; Marone et al. 2022; Patocchi et al. 2009; Soriano et al. 2009; Zhao et al. 2018).

Foot and Crown Rot and Fibrous Root Rot caused by *Phytophthora* species

Phytophthora is a cosmopolitan oomycete genus (Robin and Guest 1994; Savita and Nagpal 2012) comprising species with either a narrow or a wide range of host plants, and occurring in both agricultural and forest ecosystems (Erwin and Ribeiro 1996; Sims and Garbelotto 2021).

Phytophthora species cause two of the most serious and economically important soilborne diseases in citrus crops worldwide, known as Foot and Crown Rot and Fibrous Root Rot, affecting trunk and root, respectively (Fig. 2) (Cacciola and Magnano di San Lio 2008).

The specific symptoms of the Foot and Crown Rot are cankers and gummosis at the base of the trunk, including the collar (crown) (Cacciola and Magnano di San Lio 2008). In detail, gum exudations appear from longitudinal cracks of the bark around necrotic areas (Fig. 2a–e), which show a distinct water-soaked discoloration. Additionally, the dead bark turns soft and sloughs off the central cylinder below and a callous is formed around the edges of the lesion (Cacciola and Magnano di San Lio 2008). When the above-described canker affects more than 50% of the circumference of the trunk, the plant shows symptoms of decay to the canopy, which include leaf chlorosis, little leaves, phylloptosis, dieback of twigs, small and poor colored fruit, offspring fruit production, twig dieback and withering of leaves during periods of drought (Cacciola and Magnano di San Lio 2008). Less frequently, gummosis can be observed on stem and branches of the scion (Fig. 2a). This aerial infection is caused by rain splashing and occurs mostly when grafting is close to the soil.

Table 1 Studies related to biotechnological approaches for the selection of Mal Secco resistant/tolerant genotypes

Biotechnological approach	Mal Secco tolerant/resistant genotypes	Study
In vitro selection	'Variant 1.117' from the 'Villafranca' lemon	Nadel and Spiegel-Roy (1987)
	'Femminello-S'	Gentile et al. (1992)
	'Kütdiken'	Baş and Koç (2006)
Somatic hybridization	'Valencia' (sweet orange + 'Femminello' lemon)	Tusa et al. (1990)
	'Hamlin' (sweet orange/ 'Milam' lemon + 'Femminello' lemon)	Tusa et al. (1992), Tusa (1996)
Genetic transformation	two transgenic lemon clones of 'Femminello Siracusano'	La Malfa et al. (2007)

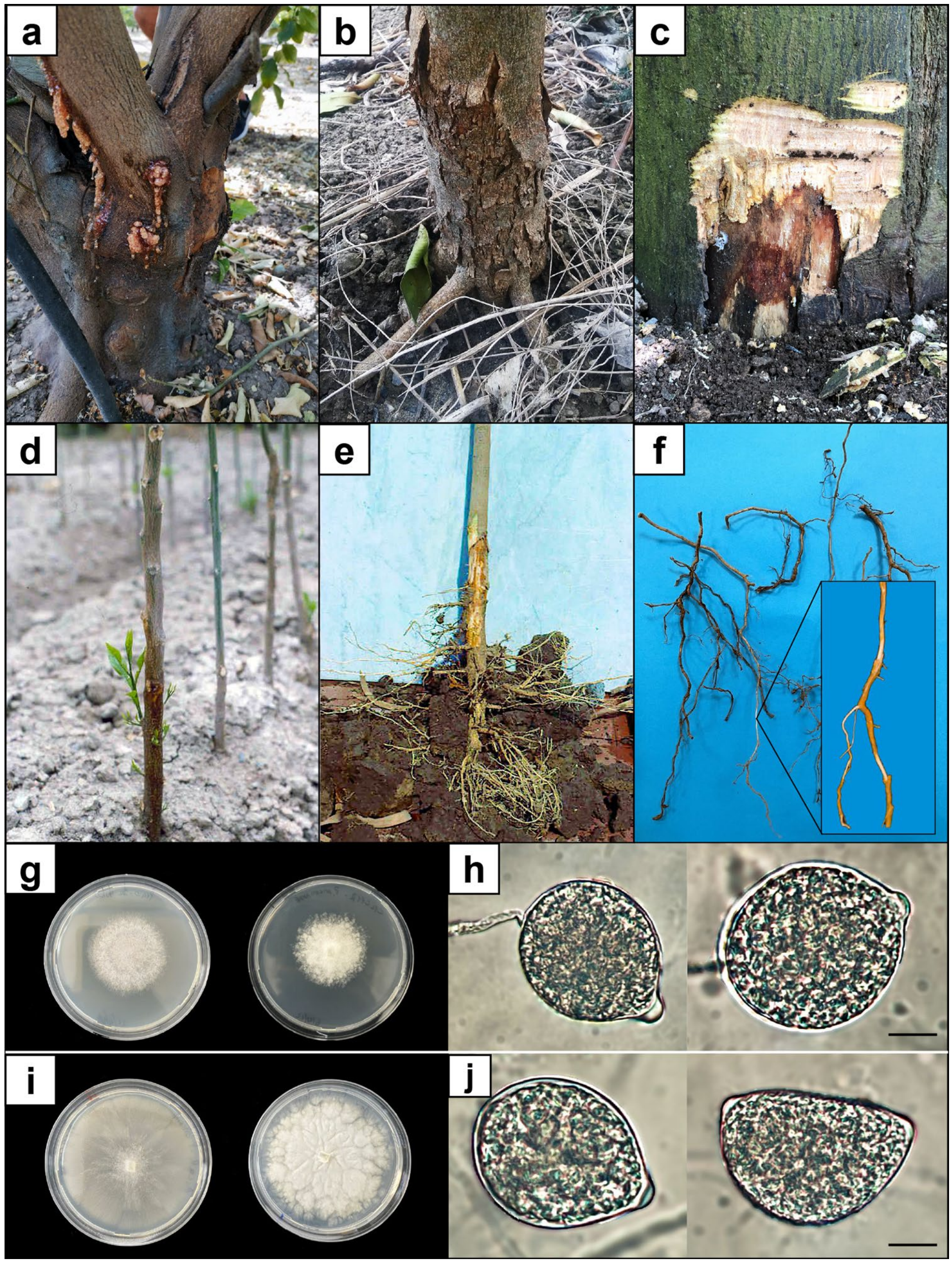

Fig. 2 **a**, **b** and **c**, Symptoms of Foot Rot and gummosis of the trunk on citrus trees in commercial orchards (Sicily, Italy); **d** and **e**, Gummosis of stem and Crown Rot on citrus saplings from a traditional local nursery (Sicily, Italy), the widespread use of containers for producing citrus saplings has greatly reduced the incidence of these diseases in commercial nurseries; **f**, Fibrous Root Rot; **g**, seven-day-old cultures of *Phytophthora nicotianae* isolate T3-B-K1A grown on V8A (left) and PDA (right) at 25 °C, with the typical stolonyferous colony morphology; **h**, papillate globose sporangia of *P. nicotianae* (scale bar: 25 µm); **i**, seven-day-old cultures of *Phytophthora citrophthora* isolate Ax1Ar grown on V8A (left) and of PDA (right) at 25 °C, with stellate to petaloid colony morphology; **j**, papillate (right) and bi-papillate sporangia of *P. citrophthora* (scale bar: 25 µm)

In the Fibrous Root Rot the thin roots slough their cortex leaving only the white thread-like stele, which gives the root system a stringy appearance (Fig. 2f) (Cacciola and Magnano di San Lio 2008). The plant, then, reacts to the infection by forming new rootlets. However, in advanced stages of the disease, the production of new roots cannot keep up with the rate of death of fibrous roots. In this disease stage, the tree is unable to maintain an adequate uptake rate of water and minerals and, at the same time, it lacks healthy tissue for storing nutrient reserves (Cacciola and Magnano di San Lio 2008). Consequently, symptoms of canopy decay, reduction of fruit size, loss of leaves and twig dieback, start to affect the plant (Dwiastuti 2020; Graham and Timmer 1992).

The main kind of propagules responsible for *Phytophthora* infections are zoospores, water-motile and biflagellate agamic spores released by specialized structures known as sporangia. Production of sporangia is mediated by the presence of water (Fig. 2h, j) (Bassani et al. 2020; Cacciola and Magnano di San Lio 2008). Sporangia are the structures responsible for disease transmission to other plants (alloinfection) and for spread to different portions of infected trees (autoinfection). Typically, once zoospores are produced and released by sporangia, they swim toward the susceptible tissue of the host, lose their flagellum, encyst and germinate, starting the infective process (Judelson and Blanco 2005). Zoospores can infect any part of the plant. However, wounds may be necessary for infection of the trunk, branches and roots, while zoospores germ tube can penetrate fruits, leaves, shoots and green twigs directly even in absence of wounds (Cacciola and Magnano di San Lio 2008). Sporangia can also germinate directly forming germ tubes that penetrate the host plant tissues.

Other kinds of propagules that can cause infection are long-lasting resistant structures, such as chlamydospores (thick-walled large resting spores) and oospores (sexual spores) (Judelson and Blanco 2005; Jung et al. 2018). Natural infections are mostly caused by zoospores and rarely by other kinds of propagules (Cacciola and Magnano di San Lio 2008; Klotz and De Wolfe 1960). The primary source of inoculum is the rhizosphere, where the pathogen survives in the form of chlamydospores and oospores; the greater amount of inoculum is in the uppermost layer of the soil. Additionally, the infected rootlets and fruits are sources of secondary inoculum, which is represented by sporangia (Cacciola and Magnano di San Lio 2008).

The most common *Phytophthora* species causing these diseases in Mediterranean basin are *P. nicotianae* (Fig. 2g, h) and *P. citrophthora* (Fig. 2i and j). *P. nicotianae* is more active in warm conditions and attacks mainly the rootlets, while *P. citrophthora* is mainly associated to trunk rot (Alvarez et al. 2009; Dirac et al. 2003; Ippolito et al. 2002; La Spada et al. 2022).

In addition to the use of chemicals, which is the most effective strategy to control diseases caused by *Phytophthora* (Foot and Crown Rot and Fibrous Root Rot), management is commonly integrated by specific agronomic practices, such as grafting plants into *Phytophthora*-tolerant rootstocks and appropriate water and soil management. (Cacciola and Magnano di San Lio 2008).

Although high virulent *Phytophthora* species, such as *P. nicotianae*, are markedly able to manipulate host tolerance by the secretion of various pathogenic effectors (La Spada et al. 2020; Wang and Jiao 2019), the use of resistant rootstocks is still the most safe and long-term solution to control *Phytophthora* diseases (Kunta et al. 2020). Unfortunately, rootstock resistant to Foot Rot may not be resistant to Root Rot as well, and vice versa (Cacciola and Magnano di San Lio 2008; Kunta et al. 2020). For instance, commonly employed rootstocks including trifoliate orange and 'Swingle' citrumelo are highly tolerant to Root Rot, but susceptible to Foot Root (Graham 1990). Conversely, sour orange (*C. aurantium*) and 'Carrizo' citrange are tolerant to Foot Rot, but susceptible to Root Rot (Graham and Timmer 1992). An additional severe limitation related to the use of *Phytophthora*-resistant rootstocks arises from the mandatory management of other serious citrus diseases, such as the citrus tristeza virus (CTV), a lethal and destructive disease affecting citrus trees grafted on sour orange (Dawson et al. 2015). The management of CTV has resulted in the substitution of sour orange with other CTV tolerant rootstocks, mainly 'Carrizo' citrange (Garnsey et al. 1987). In the Americas and Spain, the spread of or the threat posed by Huanglongbing (syn. Citrus Greening), a disease caused by three phloem-inhabiting, Gram-negative bacteria known as '*Candidatus* Liberibacter asiaticus', '*Candidatus* Liberibacter americanus', and '*Candidatus* Liberibacter africanus', to which all most popular CTV-tolerant rootstocks are susceptible (Albrecht et al. 2012; Dala-Paula et al. 2019), has triggered the search for Huanglongbing-tolerant rootstocks that are currently under evaluation (Alves et al. 2021; Arjona-López et al. 2022; Bowman and Albrecht 2020; Kunwar et al. 2021). No information is yet to be available on the susceptibility of these new rootstocks to *Phytophthora*.

Regarding soil and water management, beneficial orchard management practices should be designed to minimize those conditions that are favorable to *Phytophthora* infection. For instance, removing soil and weeds from around the root collar creates unfavorable conditions for gummosis, because it prevents the accumulation of moisture on the bark surface thus decreasing the incidence of new infections and facilitating the healing of cankers. Raised soil beds avoid the burying of the collar and further contributes to minimize soil waterlogging under the tree canopy (Cacciola and Magnano di San Lio 2008; El-Otmani 2006; Schillaci and Caruso 2006). Given the aquatic nature of *Phytophthora* spp. in their infectious phase, it goes without saying that a rational irrigation that avoids prolonged waterlogging conditions can drastically reduce the proliferation of propagules and, consequently, lower infection rates (Cacciola and Magnano di San Lio 2008).

Lastly, in the last decades, the incidence of Phytophthora Trunk Gummosis and Root Rot in citrus nurseries (Fig. 2d, e) in Italy has been substantially reduced by the use of sterile plastic containers to grow the plants combined with localized drip irrigation and the use of mulch or gravel on the soil bed to prevent soil splashing.

Fungal and oomycete diseases affecting citrus fruits in pre-harvest

Brown Rot caused by *Phytophthora* species

Phytophthora species are also the causative agents of a severe decay, known as Brown Rot, affecting citrus fruits in the field, although latent infections may manifest themselves in post-harvest fruits after an incubation period of 10–15 days at low temperature (Cacciola and Magnano di San Lio 2008). Additionally, secondary infections may also occur during post-harvest. In Brown Rot in the field, propagules of *Phytophthora* spp. in the soil are splashed by rain and/or irrigation to fruits hanging on the lower canopy of the trees (Cacciola and Magnano di San Lio 2008; Ismail and Zhang 2004). Because of thunderstorms or hurricanes, propagules may reach even the upper part of the canopy.

The initial phase of the disease is characterized by a light discoloration of affected areas on the fruit surface, but as decay progresses, lesions becomes light brown, firm and leathery (Fig. 3a–d). Under conditions of high humidity, decay spreads rapidly in the fruits and a white mycelium appears on the infected areas. Fruits with Brown Rot have a rancid stink (Cacciola and Magnano di San Lio 2008; Feld et al. 1979) and can either fall to the ground or remain attached to the canopy (Fig. 3a, c) where they, eventually, mummify. Fruit Brown Rots is often associated to Leaf and Twig Blight.

Similarly to Foot and Crown Rot and Fibrous Root Rot, the main *Phytophthora* spp. associated to Brown Rot are *P. citrophthora* and *P. nicotianae* (Fig. 3d, e). Other *Phytophthora* species associated to Brown Rot include *P. prodigiosa* and *P. mekongensis*, which were recovered from symptomatic pomelo (*C. maxima*) fruits in Vietnam (Crous et al. 2017; Puglisi et al. 2017), as well as *P. cactorum*, *P. citricola* sensu lato, *P. hibernalis* and *P. syringae*, which colonize mainly detached fruits on the ground (Cacciola and Magnano di San Lio 2008).

The management of Brown Rot relies mainly on agronomical interventions, such as the pruning of the lower part of the canopy (tree skirting), a practice that eliminates those low hanging fruits and leaves, which would otherwise easily be reached by infested water splashes. This practice is often associated with the chemical treatment of the canopy employing phosphorous acid derivatives (mainly Fosetyl-Al) or copper-based products (Cacciola and Magnano di San Lio 2008; Ismail and Zhang 2004). Another agronomic practice to prevent fruit Brown Rot is controlled inter-row grassing to reduce soil splashing. In the last years, severe epidemic outbreaks of fruit Brown Rot have occurred in southern Italy because of Medicanes or Mediterranean cyclones. In the coming years and due to climate change, the frequency of these weather events is expected to increase in the Mediterranean basin (Hochman et al. 2022).

Anthracnose by *Colletotrichum* species

Colletotrichum is one of the most important genera of plant pathogenic fungi, responsible for several diseases in many crops worldwide (Cacciola et al. 2020; Cai et al. 2009; Cannon et al. 2000, 2012; Gomes et al. 2021; Shu-he et al. 2021; Udayanga et al. 2013). *Colletotrichum* species were recently included in the list of the ten most important plant pathogenic fungi in the world (Dean et al. 2012; Shu-he et al. 2021). Agricultural production losses caused by

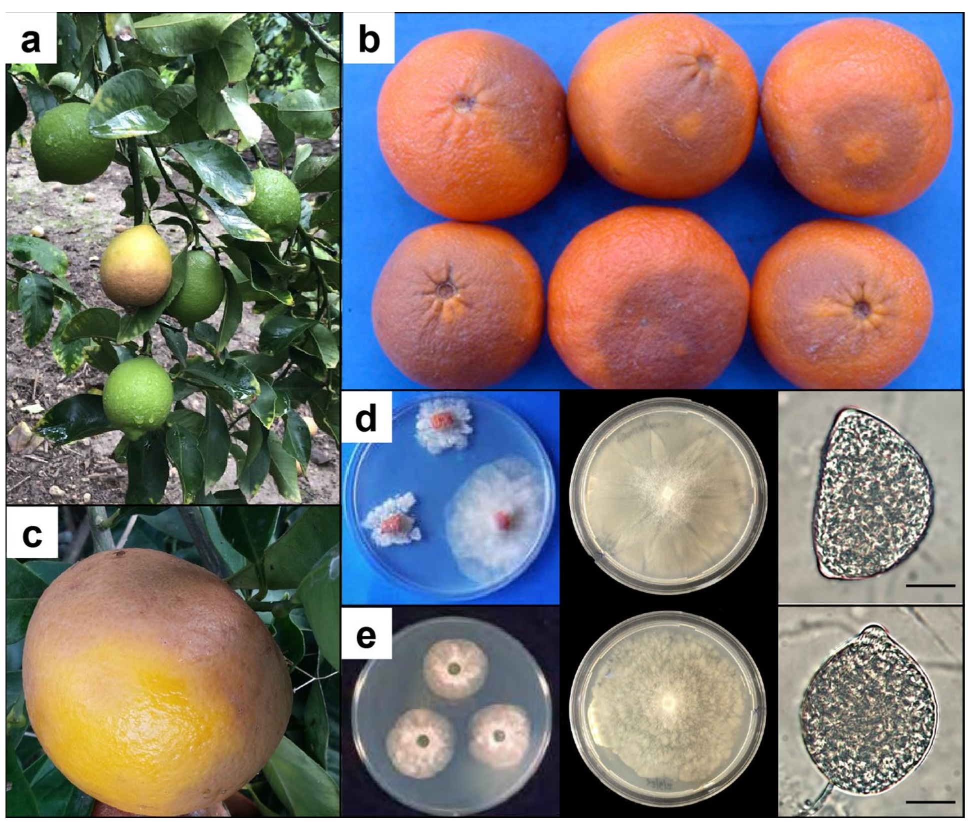

Fig. 3 Symptoms of Fruit Brown Rot (a-c) by *Phytophthora* species on citrus from commercial orchards (Sicily, Italy) both in field (**a** and **c**) and after harvesting (**b**); **d**, (from left to right) direct isolation of *Phytophthora citrophthora* and *Phytophthora nicotianae* from fruit peel, pure culture on V8A with a stellate to petaliform colony morphology and bi-papillate sporangium of *P. citrophthora* (scale bar: 25 µm); **e**, (from left to right) isolation of *P. citrophthora* from soil by leaf baiting, pure culture on V8A with the typical stoloniferous colony morphology and papillate globose sporangium of *P. nicotianae* (scale bar: 25 µm)

Colletotrichum spp. involve staple food crops growing in developing countries throughout the tropics and subtropics (Dean et al. 2012; Shu-he et al. 2021). *Colletotrichum* species can infect a multitude of plant genera (Damm et al. 2012a, b; Farr et al. 2006; Perfect et al. 1999; Shu-he et al. 2021), causing Anthracnose disease and postharvest decay on a wide range of tropical, subtropical and temperate fruits, grasses, vegetable crops and ornamental plants (Bernstein et al. 1995; Cacciola et al. 2012, 2020; Damm et al. 2012b; De Silva Dilani et al. 2017; Freeman and Shabi 1996; Lima et al. 2011; López-Moral et al. 2020; Shu-he et al. 2021; Talhinhas et al. 2018).

The most important disease imputed to *Colletotrichum* species in citrus fruits is Anthracnose, a serious and global limiting factor of food production globally (Khanchouch et al. 2017; Wang et al. 2021). Pre-harvest Anthracnose reduces yield, while post-harvest Anthracnose affects fruit quality, with negative consequences on fruit export and marketability (Fig. 4) (Wang et al. 2021).

The major *Colletotrichum* species involved in Anthracnose of citrus fruits in the Mediterranean basin are *C. gloeosporioides* and *C. karsti* (Ben Hadj Daoud et al. 2019; Khanchouch et al. 2017). The etiology of the disease is strictly related to early infections in field, which immediately cause the first product losses by colonizing not only dead and senescent leaves, but also twigs and fruits (Riolo et al. 2021). In turn, infected plant parts and fruits support the production of acervuli with abundant conidia that are then dispersed by rain splashes to developing fruits. Once conidia reach the fruit surface, they germinate to produce appressoria and quiescent infections, which usually become active at fruit maturity. When quiescent infections become active, they progress rapidly leading to death of the infected tissue and to rapid sporulation by the pathogen on such necrotic portions of the fruit (Brown 1975; Naqvi 2006; Timmer et al. 1998a). Lesions on the fruit surface remain firm, brown to brownish black and, in long term storage, the affected peel eventually develops a soft rot (Naqvi 2006).

The major strategy for the control of *Colletotrichum* Anthracnose includes actions aiming at reducing the presence and dispersion of inoculum of the pathogen. To this aim, growers employ agronomical practices such as the pruning of dead twigs from citrus trees and the removal of

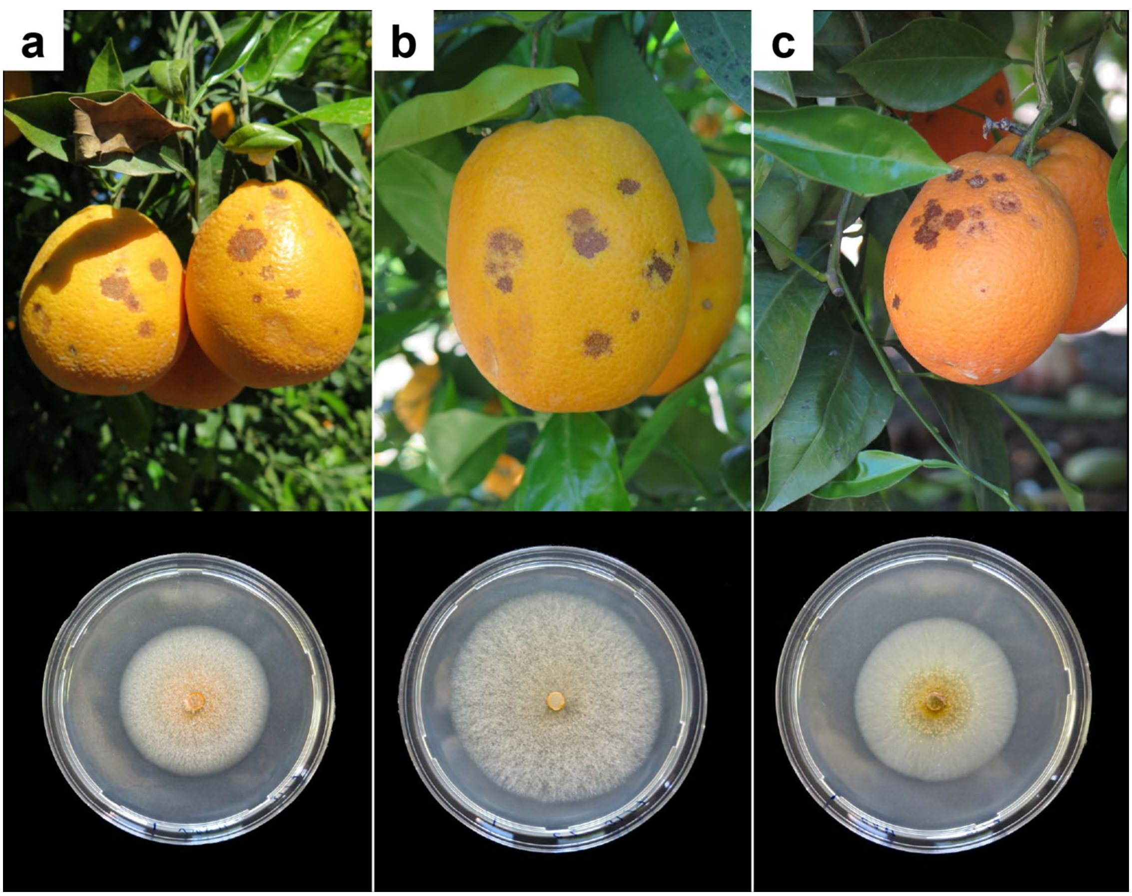

Fig. 4 Symptoms of Anthracnose by *Colletotrichum gloeosporioides* and seven-day-old pure cultures grown on PDA medium at 25 °C of the respective isolated strain: brown and brownish black spots caused by *C. gloeosporioides* isolates C1aT0 (**a**), C2k (**b**) and C3w (**c**)

fallen fruit from the grove in association with the spraying of chemicals (Lombardo et al. 2023; Naqvi 2006).

Brown spot by *Alternaria alternata*

Alternaria Brown Spot (ABS) is one of the most important diseases of tangerines and their hybrids, worldwide (Arlotta et al. 2020). It is caused by the tangerine pathotype of the fungus *Alternaria alternata*, a typical necrotrophic pathogen (Fig. 5f, g) (Khanchouch et al. 2017; Peever et al. 2004).

ABS is prevalent in citrus production areas with a Mediterranean climate, characterized by cool, humid winters and hot, arid summers. It was firstly reported on 'Emperor' mandarin in Australia in 1903, and subsequently it was detected in the Americas, the Mediterranean basin, South Africa, Iran and China affecting mainly 'Fortune' and 'Nova' mandarin hybrids (Aglave 2018; Bassimba et al. 2014; Elena 2006; Gai et al. 2021; Garganese et al. 2016; Khanchouch et al. 2017; Solel 1991). In Europe, it has been reported in Greece, Italy and Spain. In Italy and Spain, its emergence was concomitant to the diffusion of the cultivar 'Fortune' (Khanchouch et al. 2017).

Alternaria Brown Spot attacks young fruits, leaves, shoots and twigs, producing brown-to-black lesions surrounded by a yellow halo (Fig. 5a–e) (Dewdney 2021). The halo is caused by the fungal ACT-toxin (ACTT), which induces necrotic lesions on fruits and young leaves and causes defoliation and fruit drop in susceptible citrus genotypes (Arlotta et al. 2020; Khanchouch et al. 2017). Symptoms on fruits include necrotic brown circular lesions that may vary in size. Mature lesions have a corky appearance, and, in older lesions, the center may dislodge leaving tan-colored pockmarks (Akimitsu et al. 2003; Khanchouch et al. 2017). Fruits can be infected in all developmental stages, but their susceptibility is higher in the first four months following petal fall. Spring infections on young fruits may lead to premature fruit drop. Early fruit drop is common, especially if infection has occurred shortly after petal fall (Khanchouch et al. 2017). The disease represents a limiting factor for the production of mandarin or tangerine-like cultivars such as 'Fortune', 'Dancy', 'Minneola', 'Orlando', 'Nova', 'Guillermina', 'Clemenpons', 'Esbal', 'Page', 'Lee', 'Sunburst', 'Encore', 'Murcott', 'Michal', 'Winola', 'Ponkan', 'Emperor', 'Tangfang' and 'Primosole' (Khanchouch et al. 2017). Conversely, the hybrid mandarin 'Orri' is resistant (Barry et al. 2015).

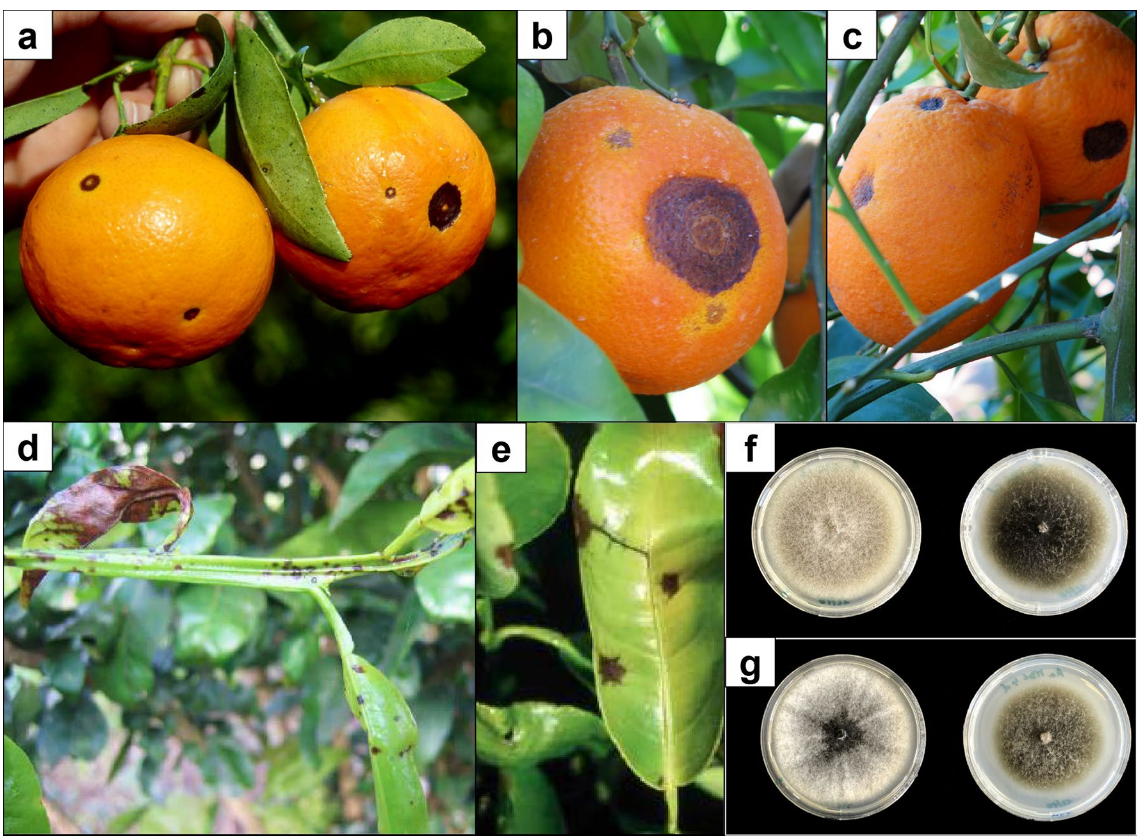

Fig. 5 Symptoms of Alternaria Brown Spot (ABS) on citrus fruits (**a**, **b** and **c**), shoots (**d**) and leaves (**e**) from a commercial orchard (Sicily, Italy); seven-day-old pure culture of the *Alternaria* isolates Aa1 (**f**) and Aa2 (**g**) grown on PDA (left) and MEA (right) at 25 °C

Although control of ABS is still largely focused on the application of chemical active substances (see section "Traditional and new promising strategies for the management of citrus diseases incited by fungi and oomycetes in the citrus supply chain"), the reduction of damages achieved is often unsatisfactory (Cuenca et al. 2016). The last aspect forces growers to replace susceptible cultivars, such as 'Fortune' or 'Nova' mandarin hybrids, with resistant accessions, or to avoid planting of susceptible cultivars in areas were environmental conditions are conducive to infections (Cuenca et al. 2013). Thus, genetic resistance remains as the best option for disease control (Bhatia et al. 2003; Peres and Timmer 2006). Because of constraints in most mandarin reproductive systems, such as polyembryony, breeding programs to obtain ABS-resistant hybrids have to include an ABS-susceptible cultivar as a parent (Cuenca et al. 2016). In this respect, many susceptible cultivars, including 'Fortune', 'Murcott', 'Ponkan', 'Dancy', 'Minneola', 'Nova', 'Fairchild', 'Fremont', 'Page', 'Orlando', 'Pixie' and 'Daisy' have been used as parents in successful resistance breeding programs, worldwide (Froelicher et al. 2012; JinPing et al. 2009; Navarro et al. 2012; Recupero et al. 2005; Schinor et al. 2012; Williams 2012).

Septoria Spot of citrus

Septoria Spot of citrus (*Septoria citri* and other *Septoria* species of the *S. protearum* species complex) is a foliar and fruit disease affecting all citrus species. The most relevant symptoms are on fruit. It causes rind blemishes, compromising the marketability of fresh fruit. On mature fruit symptoms consist of large (more than one cm diameter), often confluent, depressed brown to black, sunken blotches extending into the albedo (Fig. 6a, b). In case of severe infections, fruits develop an off-flavour and drop prematurely (Fig. 6c). Symptoms may not appear until postharvest. Another syndrome caused by *S. citri* or closely related species of *Septoria* are reddish brown pits, 1 to 2 mm in diameter, extending not deeper than the flavedo (Agosteo 2002). Septoria Spot is often misdiagnosed with Anthracnose or Brown Spot as symptoms of these diseases are similar and in culture on agar media *S. citri* grows more slowly than *A. alternata* and *Colletotrichum* species, which sometimes occur simultaneously on the same lesion (Fig. 6c, d). However, infections by *Septoria* can be distinguished by those caused by either *Alternaria* or *Colletotrichum* even at the stereomicroscope as *Septoria*, differently from the other two fungi, forms pycnidia on the necrotic lesions of the rind. Severe outbreaks of Septoria Spot were observed on mature fruits of late ripening sweet orange cultivars in Sicily as a consequence of hailstorms. Menge (2000) reported the disease is more severe in years with high rainfall levels and low or rapidly fluctuating temperatures. *Septoria citri* survives on citrus trees on dead twigs and leaves as a saprobe. Although it is ubiquitous in most citrus growing areas, including the Mediterranean region, it is considered a quarantine organism in Western Australia and some countries of East Asia, such as South Korea and Vietnam. Management strategies of Septoria Spot are substantially the same applied for Anthracnose.

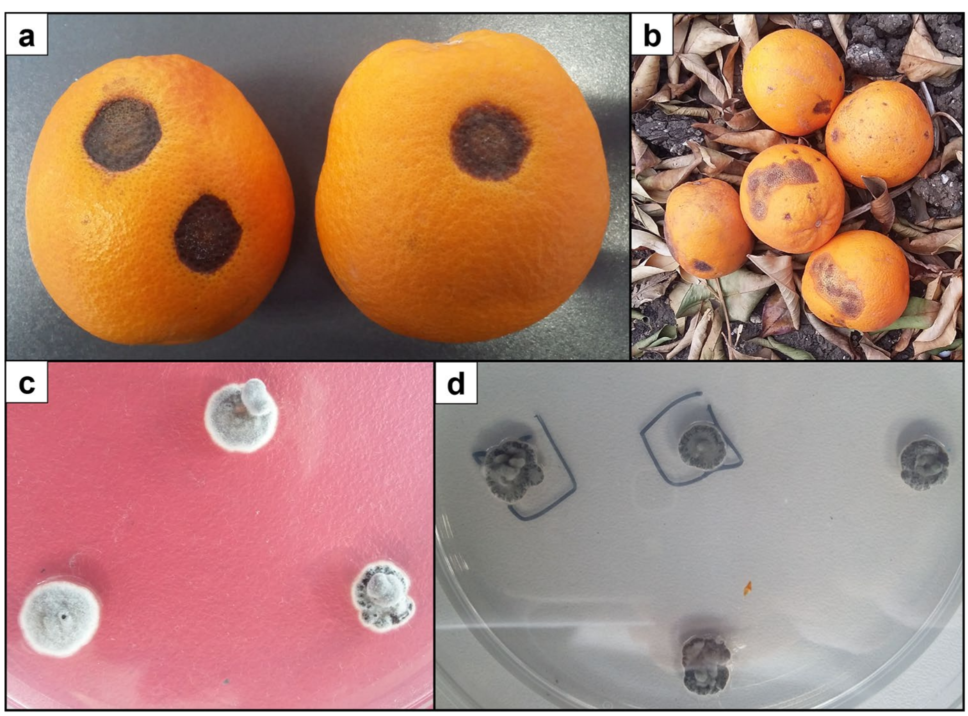

Fig. 6 Symptoms of Septoria Spot on fruits of sweet orange 'Tarocco Meli' from a commercial orchard in Sicily (**a**); fruits of sweet orange 'Tarocco Meli' affected by Septoria Spot fallen to the ground (**b**); colonies of *Septoria citri* on PDA, after 15 days incubation at 24 °C (**c** and **d**)

Citrus Black Spot by *Phyllosticta citricarpa*

Phyllosticta citricarpa (teleomorph: *Guignardia citricarpa*) is a quarantine pathogen listed in the Annex II Part A of the Commission Implementing Regulation (EU) 2019/20724. The Commission Delegated Regulation (EU) 2019/17025 also listed *P. citricarpa* as a priority pest. It is included in the EPPO A1 List (EFSA Panel on Plant Health et al. 2018; EPPO 2020). *Phyllosticta citricarpa* is also a quarantine organism in the USA (Schirmacher et al. 2019). The major disease associated with this pathogen is Citrus Black Spot (CBS), a foliar and fruit decay affecting the majority of *Citrus* species (Baldassari et al. 2008; EFSA 2014a, b; EPPO 2020; Kotzé 1981; Paul et al. 2005). CBS is present in Asia, Australia, South Africa and South America and recently has been reported from Tunisia (Boughalleb-M'Hamdi et al. 2020). In the last few years, repeated interceptions of *P. citricarpa* in citrus fruit stocks from South Africa and Argentina at entry points of the European Union (EU) have resulted in the temporary suspension of the import of citrus fruit from these countries. *Phyllosticta citricarpa* has also been intercepted at the EU frontier in a stock of sweet orange fruits imported from Egypt, where the disease was reported to be established (Khalil et al. 2022).

Spread of the pathogen responsible for CBS occurs via spores, including both windborne ascospores produced in pseudothecia (ascocarps) and waterborne conidia produced in pycnidia (Guarnaccia et al. 2017).

Ascospores are considered the primary source of inoculum in the CBS disease cycle, while conidia in rainwater are mostly responsible for the short downward dispersal of the pathogen (Guarnaccia et al. 2017; Spósito et al. 2011). Alternate wetting and drying cycles of the leaves combined with mild to warm temperature fluctuations are favorable conditions for maturation of pseudothecia and ascospore (Fourie et al. 2013; Guarnaccia et al. 2017; Hu et al. 2013).

CBS is associated with various symptoms on fruits (Guarnaccia et al. 2019; Kotzé 1981). The most commons are 'hard spots' (Fig. 7a, b), which are characterized by sunken, pale brown necrotic lesions with a dark reddish brown raised border, often containing pycnidia (EPPO 2020; Guarnaccia et al. 2017, 2019). Further symptoms are: (i) virulent spots, which are sunken necrotic lesions without defined borders mostly on mature fruits; (ii) false melanose, consisting of small black pustules usually in a tear stain pattern; (iii) freckle (Fig. 7c), cracked or speckled spot (Guarnaccia et al. 2019).

Leaf and twig symptoms rarely occur on sweet orange, mandarin and other commercial citrus species, but they are frequently reported on lemons. They appear as round, small, sunken necrotic lesions with a yellow halo (Fig. 7d) (Guarnaccia et al. 2019; Kotzé 1981).

Temperature is a crucial factor for disease development. Rapid temperature increments, typically from 20° to 27 °C, when fruits are ripe stimulate the appearance of CBS symptoms and lead to formation of a significant number of fruit lesions (Guarnaccia et al. 2019; Lee and Huang 1973). High light intensity can further facilitate fruit lesion development, thus the side of the canopy more exposed to sunlight typically shows more symptoms (Guarnaccia et al. 2019). Old age and physiological stress also appear to facilitate the development of CBS (Guarnaccia et al. 2019; Kotzé 1981).

A precise diagnosis of *P. citricararpa* is complicated by two main factors. First, necrotic spots are generic symptoms that can be caused by other *Phyllosticta* species (Guarnaccia et al. 2019; EFSA Panel on Plant Health 2014; EPPO 2020) and even by other ascomycetes (e.g. *Septoria citri* and *Cytosporina citriperda*). Second, the wide morphological and molecular similarities among species in the genus *Phyllosticta* (e.g. *Phyllosticta paracapitalensis* and *Phyllosticta paracitricarpa*) (Guarnaccia et al. 2019; Santa Olga Cacciola, personal communication). For instance, both *P. citricarpa* and *P. paracitricarpa* can cause CBS symptoms on citrus fruits and the two species differ from each other just for some nucleotides related to *tef1* and LSU genes (Guarnaccia et al. 2017). A range of molecular tests, including multiplex methods for the detection of different citrus pathogens simultaneously, have been developed to detect *P. citricarpa* (Ahmed et al. 2020; EPPO 2020). Nevertheless, these tests cannot distinguish *P. citricarpa* from the closely related species *P. paracitricarpa* and *P. citriasiana*. Only recently, a new real-time PCR protocol, still under validation by EPPO, apparently makes possible the exclusive detection of *P. citricarpa* by targeting the *tef1* gene (Zajc et al. 2022). There is still a need for practical, accurate, robust and cost-effective diagnostic methods for the rapid and early detection of *P. citricarpa* on imported citrus fruit stocks at international borders.

Post-harvest fungal diseases of citrus

Green and Blue Molds by *Penicillium* species

Penicillium digitatum and *Penicillium italicum* stand out as the most destructive post-harvest diseases (Bhatta 2022; Cheng et al. 2020; Kassim et al. 2020) of citrus fruits.

The geographical distribution of these two species includes all of the citrus-producing areas in the world and they have been also described in countries that only import but do not produce citrus (Frisvad and Samson 2004). Both *P. digitatum* and *P. italicum* are obligate wound pathogens that infect the fruits through peel injuries produced in the field, in the packing house or during the fruit commercialization chain (Fig. 8) (Bautista-Baños 2014; Palou 2014).

Penicillium digitatum, the causative agent of citrus Green Mold, is the more serious and widespread pathogen of the

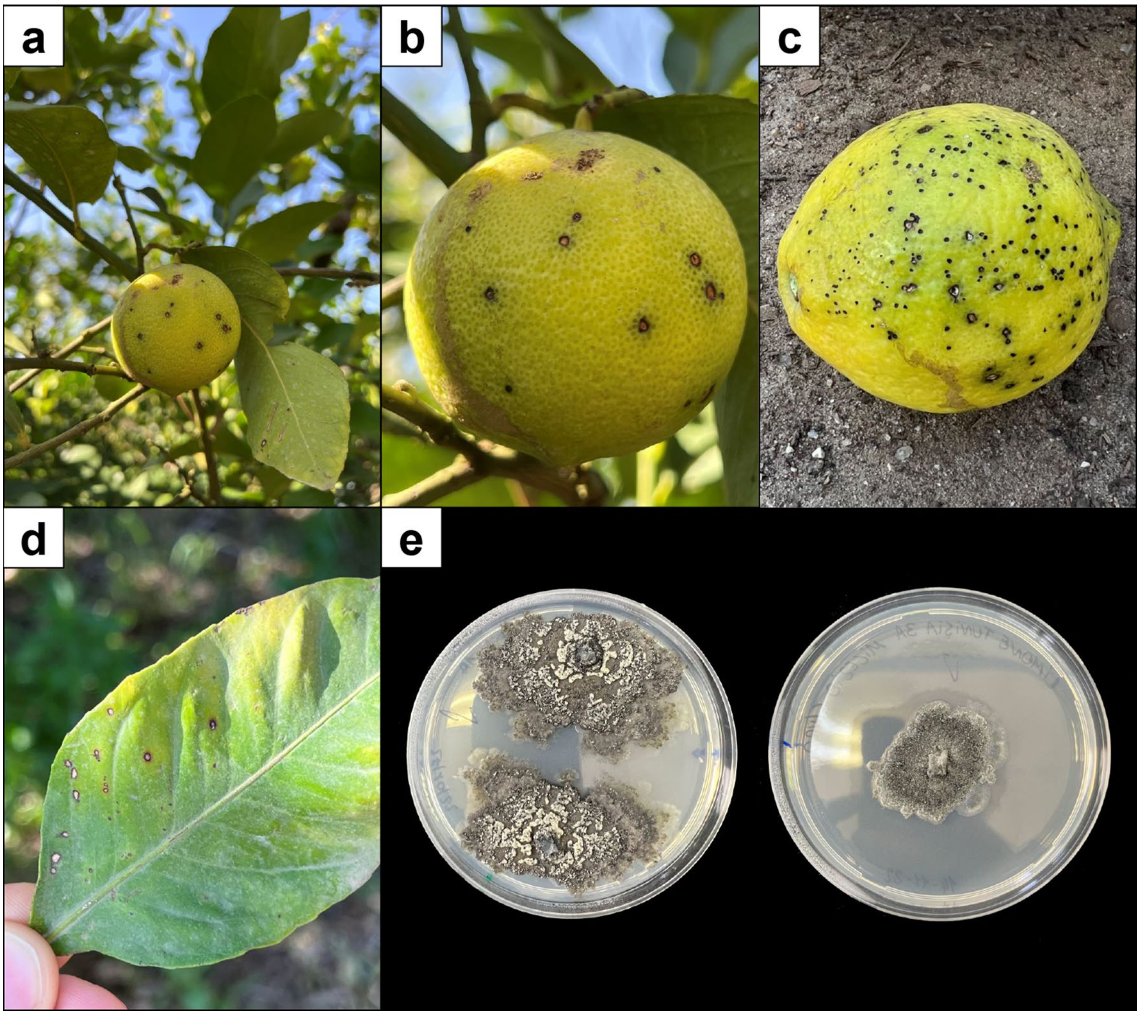

Fig. 7 **a**, **b** and **c**, Hard and freckle spots by *Phyllosticta citricarpa* on peel of mature lemon fruits from a commercial orchard (Tunis, Tunisia); **d**, hard spot lesions on lemon leaves; **e**, seven-day-old sporulating cultures of *P. citricarpa* grown on PDA medium at 25 °C

two *Penicillia* (Abo-Elnaga 2013; Kanan and Al-Najar 2008; Plaza et al. 2004; Batta 2007). This disease is considered the main cause of economic losses in citriculture, resulting in 90% of the total post-harvest losses of citrus fruits (Costa et al. 2019; Ismail and Zhang 2004; Macarisin et al. 2007; Perez et al. 2017; Vu et al. 2018).

At the early stages, wound infections from which fruit spoilage starts (La Spada et al. 2021) develop a soft area on the fruit peel surrounding the wound. This symptom is sometimes referred to as 'Clear Rot' (Ismail and Zhang 2004). Warm temperatures promote the development of a white mycelium on the soft area and shortly after (usually within three days in standard conditions), the production of green conidia commences (Costa et al. 2019; Ismail and Zhang 2004; La Spada et al. 2021; Vu et al. 2018). As the invasion of citrus peel progresses, the mycelium produces cell wall-degrading enzymes that cause a break-down of the fruit cell walls. The infection proceeds quickly, and within a few days, the entire fruit results totally molded and covered by green conidia (Fig. 8b) (Ashebre 2015; Ismail and Zhang 2004).

In order to reduce the occurrence of the disease, it is imperative to pick and carefully handle fruits in the field, minimizing the production of wounds (Palou 2014). However, the large amounts of fruit to be moved, the high labor costs and, in many cases, the lack or low availability of conscientious, skilled and well-trained teams of pickers, are often factors that limit the adoption of proper harvesting practices. Additionally, harvests should be avoided after rainfall or when fruits are wetted by free water; these conditions promote both sporulation by the pathogen and excessive turgidity of the fruits, which in turn makes fruits more susceptible to mechanical damage and subsequent infection (Eckert and Eaks 1989; Palou 2014). Furthermore, some sweet orange cultivars, e.g. 'Lempso', are particularly prone to Penicillium mold infections in the field (Fig. 8a), further complicating

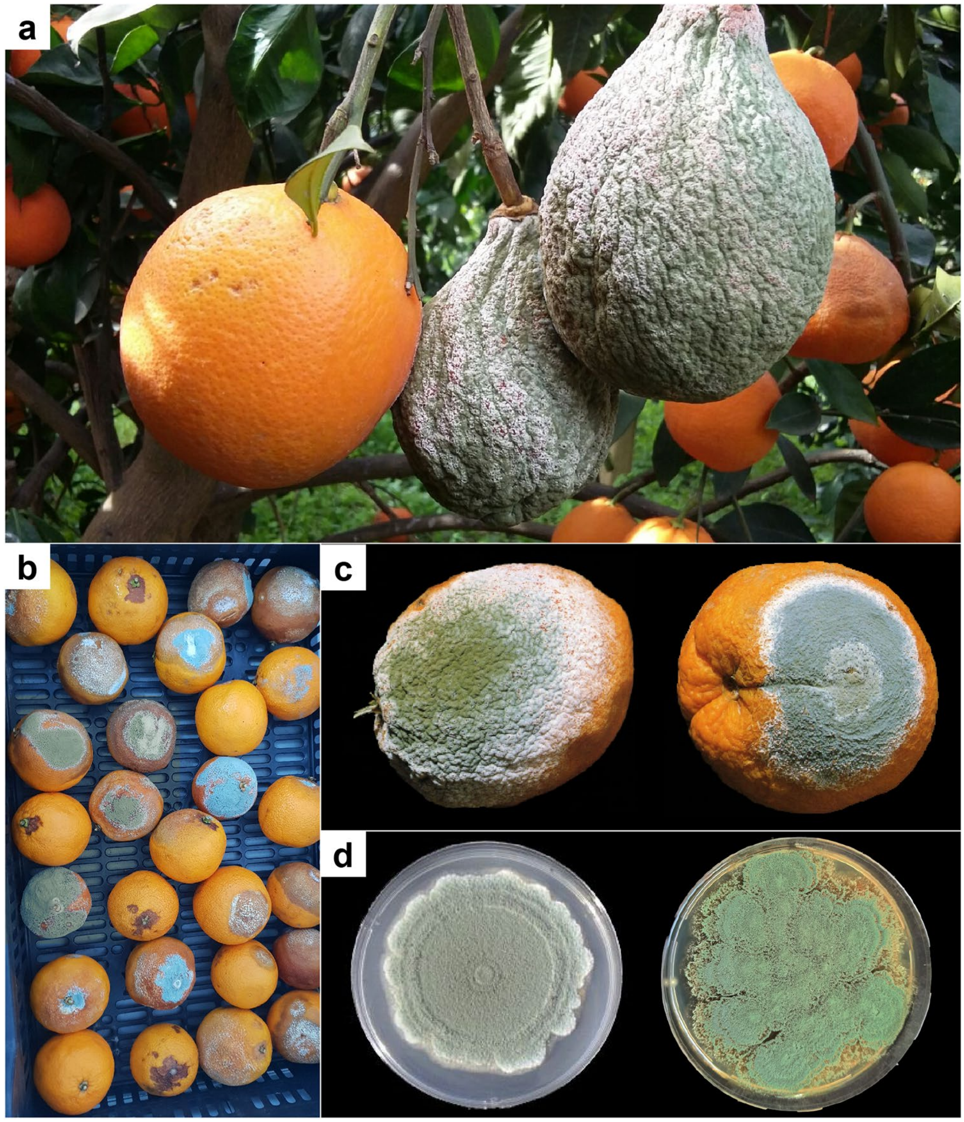

Fig. 8 **a**, **b** Sweet orange fruits affected by green (*Penicillium digitatum*) and blue (*P. italicum*) molds; **c**, severe status of decay of mature sweet orange fruits affected by green (left) and blue (right) molds (note the white mycelium at the advancing margin of the lesion and green —left—/ blue —right— conidia); **d**, seven-day-old cultures of *P. digitatum* isolate P1PP0 (left) and *P. italicum* isolate T4N0 (right) grown on PDA medium at 25 °C

disease control. One of the main causes responsible for the spread of the Green Mold in post-harvest is the lack of appropriate measures of sanitation in packing house facilities, storage rooms and containers, which result in a significant presence of inoculum (Palou 2014). Green Mold can be also caused by the spread of conidiafrom diseased fruit onto adjacent wounded fruits (Ismail and Zhang 2004).

Penicillium italicum is the second most important species affecting post-harvest citrus (Costa et al. 2019; Poppe et al. 2003); it is the causative agent of the disease knowns as Blue Mold of citrus. The organism infects citrus fruit via injuries, similarly to *P. digitatum*. Citrus Blue Mold occurs in all citrus-producing regions of the world. Initial lesions are similar to lesions caused by *P. digitatum*, but the conidia are blue in color and the area of the citrus peel, where they appear, is typically surrounded by a narrow band of white mycelium growing on the water-soaked rind. With time, the entire surface of the fruit is completely covered by conidia (Fig. 8c), then, the fruit begins to shrink and, if exposed to air, becomes a slimy shapeless mass (Bautista-Baños 2014; Palou 2014).

Blue Mold is more common in fruit held in cold storage during the summer and it can spread in packed cartons more readily than Green Mold, causing a so called 'nest' of decayed fruit (Ismail and Zhang 2004). In infected citrus fruits *Penicillium* species produce several secondary metabolites, including mycotoxins, such as patulin and rubratoxin B (Rovetto et al. 2023b).

Because of their high destructiveness, the effective control of citrus molds by *Penicillium* species is unfortunately strictly dependent on the employment of specific chemicals (see section "Traditional and new promising strategies for the management of citrus diseases incited by fungi and oomycetes in the citrus supply chain").

Sour Rot by *Geotrichum candidum* var. *citri-aurantii*

Sour Rot caused by *Geotrichum candidum* var. *citri-aurantii* is one of the most serious wound-mediated citrus diseases worldwide (Fig. 9), second in importance only to *Penicillium* molds (Ismail and Zhang 2004; Naqvi 2006). It has been reported on all citrus cultivars in the majority of citrus growing areas. It is particularly frequent in fruits in long storage at cold temperatures (Ismail and Zhang 2004; Naqvi 2006). Sour Rot is more frequent on mature to over-mature fruits characterized by the presence of a high amount of moisture on the peel surface (Ismail and Zhang 2004; Naqvi 2006).

Propagules of the fungus are typically present in the soil; they can reach the fruit surface blown by wind, in infested soil particles splashed by water, or by the direct contact of the fruit with soil (Ismail and Zhang 2004; Naqvi 2006). Further postharvest spread pathways are known, for instance contaminated fruits can spread the pathogen through drenching equipment, soak tanks, pallet bins, washer brushes, belts and conveyors, and by contact with infected fruits in storage containers (Ismail and Zhang 2004; Naqvi 2006). All infections are wound-mediated, and occur mostly in wounds that affect the albedo tissue (Ismail and Zhang 2004; Naqvi 2006). Initial symptoms are water-soaked lesions, light to dark yellow and slightly raised. In this early disease phase, the damage to the peel cuticle is distinctive and compared to what happens in fruits affected by molds by *Penicillium* spp., the peel cuticle can be easily removed from the epidermis (Ismail and Zhang 2004; Naqvi 2006). Decayed fruit tissue is typically characterized by a sour stink that attracts fruit flies, which in turn spread the pathogen to other injured fruit during storage (Ismail and Zhang 2004; Naqvi 2006). The disease develops rapidly at warm temperatures, with an optimum of about 27 °C (Ismail and Zhang 2004; Naqvi 2006).

Sour Rot could be partially prevented by sanitation control and low-temperature storage. However, chilling injury and temperature fluctuation during transport and marketing still represent the major predisposing factors (Liu et al. 2009; Mercier and Smilanick 2005).

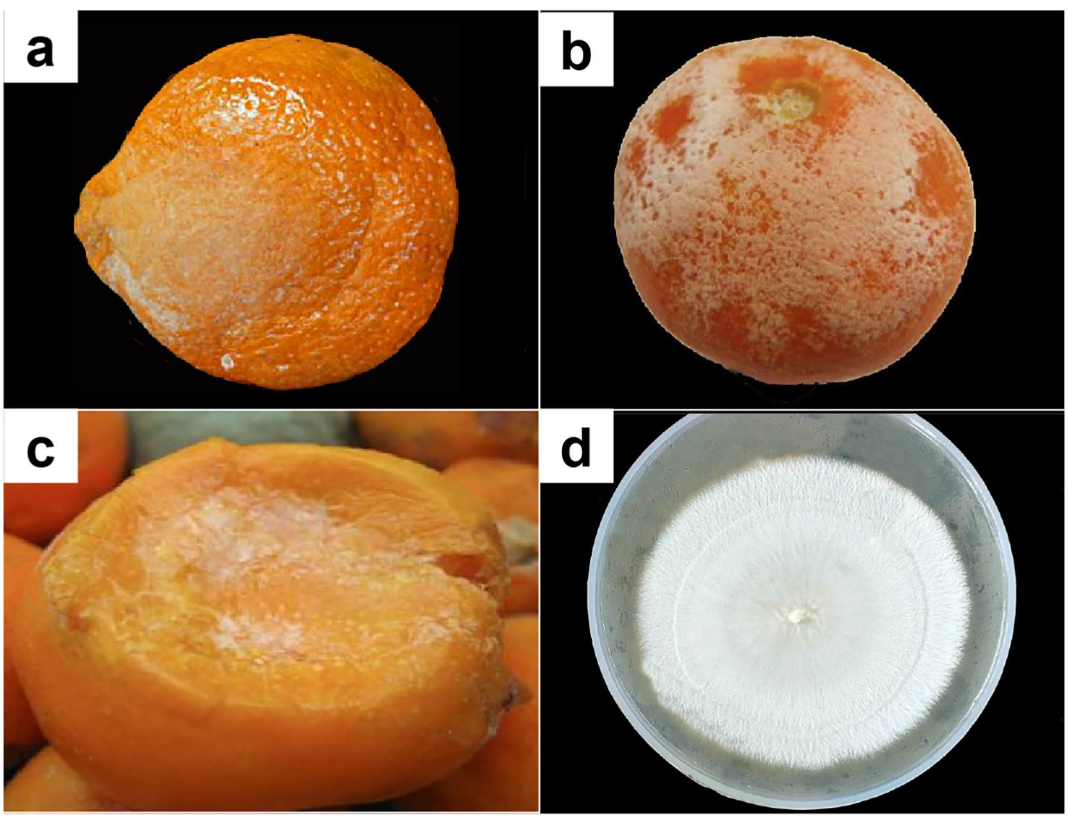

Fig. 9 **a**, **b** and **c** Mature sweet orange fruits affected by Sour Rot; **d** seven-day-old culture of *Geotrichum candidum* var. *citri-aurantii* isolate G-1N0 grown on PDA medium at 25 °C

Mycotoxins in products from citrus supply chain

The consequences related to infection by fungal pathogens do not just affect the mere quality of the produce, but can have direct consequences on the health of the consumers. It is well known that some pathogens of citrus fruits are able to produce mycotoxins whose presence in fresh fruit peels and juice pose a serious threat to human health (Awuchi et al. 2021; Fernández-Cruz et al. 2010). Mycotoxins exhibit properties of acute, subacute, and chronic toxicity in animals and/or humans; some of these have also been reported as carcinogenic, mutagenic, and teratogenic (Fernández-Cruz et al. 2010; Lu et al. 2022; Omotayo et al. 2019). Mycotoxins are secondary metabolites produced by fungi and can act as virulence and pathogenicity factors during the infection process (Masi et al. 2020; Stracquadanio et al. 2021). They can be produced before and after harvest, and their levels may increase during post-harvest, handling, and storage (Stracquadanio et al. 2021). The proliferation of fungi and the production of mycotoxins on food are favored by specific environmental factors, such as humidity, temperature, as well as by the physical and chemical composition of the plant matrix. This is one of the reasons why the presence of a mycotoxigenic fungal species is not necessarily associated with the presence of critical amounts of mycotoxins (Drusch and Ragab 2003). Additionally, variation in mycotoxin production among fungal genotypes of the same species further complicates the matter (Drusch and Ragab 2003; Logrieco et al. 1990). A major mycotoxigenic fungus in the citrus supply chain is *A. alternata* (Fernández-Cruz et al. 2010; Logrieco et al. 2009; Masiello et al. 2020; Patriarca 2016). *Alternaria alternata* produces a number of mycotoxins, including the dibenzo-α-pyrones alternariol (AOH), alternariol monomethyl ether (AME) and altenuene (ALT), altertoxin I and II (ATX-I and -II) and tenuazonic acid (TeA) a tetramic acid (Aloi et al. 2021; Barkai-Golan and Paster 2008; Fernández-Cruz et al. 2010; Magan and Olsen 2004). ALT and ATX-I were the most acutely toxic mycotoxins in mice, with a median lethal dose (LD_{50}) of 50 and 200 mg/kg, respectively; the toxicity of TeA (LD_{50} 115 mg/kg) was sub-acute, while only weak toxicity was reported for AOH and AME (LD_{50} 400 mg/kg) (Fernández-Cruz et al. 2010). Culture extracts of *A. alternata* can be mutagenic in various microbial and cell systems and carcinogenic in rats (Fernández-Cruz et al. 2010). It has also been suggested that *A. alternata* could be involved in the etiological factors leading to human oesophageal cancer in China (Dong et al. 1987; Zhao et al. 2022). Finally, ATX-1, AOH and AME have also been shown to be mutagenic (Dong et al. 1987; Scott 2001). As expected, the production of *A. alternata* mycotoxins has been detected both under natural infection conditions and in experimental inoculation trials involving different citrus fruits, including lemons (Barkai-Golan and Paster 2008; Logrieco et al. 1990), sweet oranges and tangerines (Barkai-Golan and Paster 2008; Logrieco et al. 1990; Magnani et al. 2007; Rovetto et al. 2023b; EFSA Panel on Contaminants in the Food Chain 2011).

To date, many methods are available for the detection of mycotoxins (Shi et al. 2018). Enzyme-linked immunosorbent assay (ELISA), High-performance liquid chromatography (HPLC), liquid chromatography-tandem mass spectrometry (LC199 MS/MS), gas chromatography (GC), and thin-layer chromatography (TLC) are techniques commonly used for mycotoxin analysis worldwide (Thomas et al. 2017; Magan and Olsen 2004; Shi et al. 2018; Wang et al. 2022). Beside *A. alternata, P. digitatum* can produce mycotoxins in citrus fruit. High levels of the mycotoxins patulin and rubratoxins B were detected in mummified blood orange fruits infected by this fungus (Rovetto et al. 2023b).

Recent advancements have improved the safety of food in accordance with EU and EPPO toxicological standards (Fumagalli et al. 2021). Among these, liquid chromatography coupled to mass spectrometry (LC–MS/MS) allows for the rapid, cost-effective and precise detection of mycotoxins (De Dominicis et al. 2012; Lau et al. 2003; Ostry 2008; Scott 2001; Tanaka et al. 2006). The LC–MS/MS currently represents the most flexible and effective (*i.e.* high sensitivity and selectivity) technique employed to determine contaminants by chemicals in a broad array of food matrices (De Dominicis et al. 2012). Some examples of the efficacy of these new approaches include the detection of pesticides and veterinary drug residues (widely employed in agriculture and farming), natural toxins (secondary metabolites, produced by various fungi, that can grow on several agricultural commodities both in field and during storage), environmental contaminants, processing and packaging contaminants, and spoilage markers (De Dominicis et al. 2012).

Traditional and new promising strategies for the management of citrus diseases incited by fungi and oomycetes in the citrus supply chain

To date, citrus disease management practices in the citrus supply chain, are all oriented to avoid and/or minimize disease predisposing factors through an integrated approach (Naqvi 2006). Up to date knowledge on the etiology of the diseases, especially regarding aspects related to the mechanisms of infection and the environmental conditions favoring the pathogen development, could be useful to plan 'smart' management strategies. In this respect, the adoption of minimal requirements, such as improved cultural practices, the regular monitoring of the disease appearance paired with the monitoring of weather conditions and the implementation of improved post-harvest handling, sanitation of equipment, transport and storage conditions (Naqvi 2006), could represent necessary and sufficient measures to safeguard yield and, at the same time, to guarantee the safety of the environment and of human health. For example, it is well known that a constant storage temperature 6 °C or less, almost totally inactivates the sporulation and growth of the post-harvest pathogens responsible for the majority of products losses, namely *P. digitatum*, *P. italicum* and *G. candidum* var. *citri-aurantii* (Plaza et al. 2003). However, the generalized disregard of the above-listed minimum requirements in the citrus supply chain, together with the increasingly frequent unpredictability of climatic conditions, inevitably require the adoption of 'foolproof' solutions, mostly represented by the timely application of pesticides (Naqvi 2006).

In 2019, the "pesticide world ranking per country" reported China, USA, Argentina, Thailand, Brazil, Italy, France, Canada, Japan and India in the top ten of the major consumers; in that year, these countries contributed to a global usage of about 2.0 million tons of pesticides, of which, 17.5% were fungicides (Sharma et al. 2019). Fungicides employed for the control of citrus diseases in the field include copper, commonly applied as a foliar spray to prevent citrus Brown Rot and occasionally used for reducing the sporulation of *P. tracheiphilus* in Mal Secco (Deb et al. 2020; Migheli et al. 2009). Systemic fungicides, like metalaxyl, Al ethyl-phosphyte (or fosetyl-Al) and metalaxyl-M (or mefenoxam), are also used for controlling *P. nicotianae* and *P. citrophthora* (Aparicio-Durán et al. 2021; Cacciola and Magnano di San Lio 2008; Davis 1982; Farih et al. 1981; Hao et al. 2021; Timmer and Castle 1985; Timmer et al. 1998b). In Europe, the chemical control of fruit decays occurring in pre-harvest, between post-bloom and harvest, is commonly carried out by spraying the newly registered fungicides pyraclostrobin and fludioxonil for the control of fruit diseases caused by *Alternaria* (Rots and Brown Spot) and *C. gloeosporioides* (Anthracnose) (Avenot and Michailides 2015; Jaouad et al. 2020).

As discussed above, some fruit decays, such as 'Brown Rots' by *Phytophthora* species, are often characterized by latent pre-harvest infections with symptoms being manifested later during post-harvest. The traditional management of this disease involves specific actions which begin in the field and continue to the storing stage in the warehouse. Apart from the delopyment of good science-based pre-harvest agronomical (thoughtful pruning of plants and soil management) that are known to reduce inoculum, additional treatments include the spraying of the canopy with Fosetyl-Al or copper-based products in the field (Cacciola and Magnano di San Lio 2008; Ismail and Zhang 2004) and a range of customary post-harvest measures, including the drenching of fruits with sanitation compounds such as chlorine or peroxyacetic acid (Federico La Spada, personal communication; Ismail and Zhang 2004). Fruits moved internationally are further chemically treated to control *Penicillium* spp. using compounds such as imazalil and thiabendazole (Bhatta 2022; Chen et al. 2019a; Davé et al. 1989; La Spada et al. 2021; Palou et al. 2002). The employment of fungicides has detrimental side effects for human and environmental health, including the presence of substances with acute toxicity in fruit peels (EFSA 2006, 2007, 2010, 2014b) and the accumulation in soil, water and plants, of non-biodegradable active compounds (Gikas et al. 2022; Stracquadanio et al. 2021).

Apart from the toxicological aspects related to the use of fungicides, one of the major drawbacks of their use is related to the emergence of resistant strains of the pathogen (Arslan 2015; Brent and Hollomon 2007; Davé et al. 1989; Holmes and Eckert 1999; Kanetis et al. 2007; Strange and Scott 2005). The indiscriminate and excessive use of fungicides in crops has been identified as one of the main causes behind the emergence of resistant pathogen populations (Avenot and Michailides 2015; Brent and Hollomon 2007; Da Cruz Cabral et al. 2013; Stracquadanio et al. 2021). In particular, the emergence of strains of *Penicillium* resistant to imidazole and bendimidazole, has prompted the development of several other synthetic fungicides, including fludioxonil and pyrimethanil, that are new effective and EU-approved alternatives for the chemical control of these post-harvest fruit diseases (Chen et al. 2019b; Davé et al. 1989; Eckert and Ogawa 1988; Errampalli and Crnko 2004; Kanetis et al. 2007).

Increasingly restrictive laws and regulations have reduced or prohibited the use of pesticides while promoting eco-friendly strategies of disease management (Fenta et al. 2019; Talibi et al. 2014). In accordance with the European Directive 2009/128/EC, which establishes a frame of community action for the sustainable use of pesticides in order to reduce the risks for human health while satisfying the growing request for high-quality, safe and eco-friendly products, alternative means to synthetic fungicides have been actively identified and tested (European Parliament 2009; Helepciuc and Todor 2021). These alternatives include the use of antagonistic microorganisms or of their bio-derivatives (Du Jardin 2015; La Spada et al. 2020; Stracquadanio et al. 2020; Riolo et al. 2023) as well as the use of natural substances (botanicals and other organic substances) and other natural antimicrobial compounds (El Boumlasy et al. 2021; La Spada et al. 2021; Wang et al. 2014; Yang et al. 2021). The United States Environmental Protection Agency (EPA) has defined 'Biopesticides' the pesticides derived from such natural materials as animals, plants, bacteria, and certain minerals (https://www.

epa.gov/ingredients-used-pesticide-products/what-are-biopesticides#classes). According with the definition of EPA, Biopesticides fall into three major classes: Biochemical pesticides, Microbial pesticides and Plant-Incorporated-Protectants (PIPs). A growing body of literature reports effective results using these alternative approaches in the citrus supply chain (Chen et al. 2020; Droby et al. 2002; Ferreira et al. 2020; Ghosh et al. 2016; Jagtap et al. 2012; Moraes Bazioli et al. 2019; Talibi et al. 2014; Wilson and Wisniewski 1989). Interestingly, some of these alternative methods are effective not only because of their direct action toward the pathogen, but also thanks to their ability to elicit plant (or fruit) defense responses (La Spada et al. 2020, 2021).

Below, is a list of successful alternative citrus disease management options. *Penicillium* spp. have been controlled by the application of harmless inorganic salts (Fallanaj et al. 2016; Youssef et al. 2012, 2014), of humic acid and garlic (Abo-Elnaga 2013), of seaweed extracts and plant derivatives (Bhatta 2022; Chen et al. 2019a; La Spada et al. 2021; Pangallo et al. 2017), as well as by the use of antagonist microorganisms, especially yeasts belonging to the genera *Kloeckera*, *Pichia* and several species of *Candida* (Droby et al. 2002; El-Ghaouth et al. 2000; Lima et al. 1997; Taqarort et al. 2008; Wilson and Chalutz 1989; Wilson and Wisniewski 1989). Among these, *Candida oleophila* stands out for its marked antagonistic activity toward fungal pathogens, attained in a complex way through competition for nutrients and space (Brown et al. 2000; Dukare et al. 2018; Freimoser et al. 2019; Zhang et al. 2020), production of lytic enzymes (Bar-Shimon et al. 2004) and induction of host systemic resistance (Droby et al. 2002; Dukare et al. 2018; Freimoser et al. 2019; Zhang et al. 2020). However, caution should be exerted about the actual efficacy of these recent alternative options, given that *in vivo* results are often far less promising than results obtained *in vitro*. This is the case, for instance, of applications of *C. oleophila* that did not result in the effective colonization of citrus peel by the putative biocontrol agent. (Brown et al. 2000), highlighting the importance of adopting complete testing protocols that include realistic *in vivo* experimentation. Additionally, even when both *in vivo* and *in vitro* results are promising, one has to determine if the products used are safe for humans, socially acceptable and allowed by current laws and regulations. This may be the case, for instance, of the use of processed food waste, shown to be effective, both *in vivo* and *in vitro*, in the inhibition of growth of the fungal pathogens *P. tracheiphilus*, *A. alternata*, *C. gloeosporioides, P. digitatum* and *P. italicum*, as well as of the oomycetes *P. nicotianae* and *P. citrophthora* (El Boumlasy et al. 2021).

The need to proceed 'safely' when attempting to control pre- and post-harvest decay of citrus, together with the need to limit the impact and spread of mycotoxigenic fungi, imposes the peremptorily adoption of state-of-the-art technologies and strategies of management. The early detection and correct identification of the pathogens involved represent the first prerequisites for the implementation of effective and rational integrated disease management strategies (Garrido et al. 2012; Ray et al. 2017; Santonocito et al. 2023). This is especially true for the citrus supply chain, which is affected by pathogens of quarantine concern infecting fruit, such as *Phyllosticta citricarpa* (EPPO 2020). Traditionally, fungal pathogens have been indirectly identified and detected either by the recognition of disease symptoms and/or by the microscopy-based observation of morphological structures on infected plant tissues (Agrios 2004; Erwin and Ribeiro 1996; Ray et al. 2017). Even if pure cultures are available, thanks in part by the use of selective media, the generalized similarity of morphological characters makes it extremely difficult and laborious to distinguish phylogenetically close taxa (Crous et al. 2012; Jung and Burgess 2009; Scanu et al. 2015; Scott et al. 2009; Woudenberg et al. 2013). Starting in 2004, with the adoption of a PCR based assay (Hayden et al. 2004) to identify the pathogen *Phytopthora ramorum* (Davidson et al. 2002; Swain and Garbelotto 2004), a vast range of nucleic acids-based methods are increasingly becoming valuable tools in all aspects of plant protection (Aslam et al. 2017; Biasi et al. 2016; Jung et al. 2019; Leakey et al. 2009; Mammella et al. 2011). DNA amplification-based methods make it possible to overcome the main limits of the traditional methods of identification and detection, allowing for the discrimination of closely related taxa from tiny quantity of propagules even in absence of signs or symptoms (Aslam et al. 2017; Cooke et al. 2007). The majority of official protocols for the early detection of quarantine plant pathogens mainly rely on Polymerase Chain Reaction (PCR)-based methodologies, both in its traditional (conventional PCR) and in the most advanced real-time (quantitative RT-PCR) form. PCR-based diagnostics may be inadequate for cost-effective large-scale and routine applications (Wong and Medrano 2005). In this respect, during the last years the Recombinase Polymerase Amplification (RPA) is becoming a molecular tool of choice for the rapid, specific, and cost-effective identification of pathogens (Lobato and O'Sullivan 2018; Rovetto et al. 2023a). Likewise, NGS approaches are increasingly being used in diagnostics (Del Frari et al. 2019; Johnston-Monje et al. 2017; La Spada et al. 2022; Morales-Cruz et al. 2018; Ruiz Gómez et al. 2019), even if not at the regulatory level (Aragona et al. 2022).

Conclusions

New green technologies offer practical smart and ecofriendly solutions that can increase the sustainability and safety of the citrus fruit value chain. Particularly interesting are the perspectives of innovation in the post-harvest sector, a sector that so far has relied prevalently on the efficacy of synthetic fungicides. It is likely that a decisive contribution to the modernization and adaptation of this sector to higher environmental, phytopathological and toxicological standards will come from the public and private industry research committed to the development of new biocontrol agents, natural antifungal substances, analytical methods to detect mycotoxins, edible fruit biocoating, biodegradable and recyclable fruit packaging and rapid molecular diagnostics to detect fungus and oomycete pathogens. The availability of these technical tools will make feasible an innovative integrated management strategy to reduce the impact of diseases in the citrus fruit value chain.

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