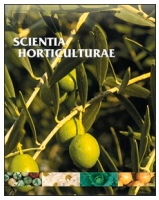
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Research Paper



Fruit cuticle composition influences susceptibility of peach (*Prunus persica)* fruit to brown rot (*Monilinia fructicola)*

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ABSTRACT

Brown rot, caused by *Monilinia* spp., is the most significant disease affecting stone fruits, including *Prunus persica* (peach). In Europe, *Monilinia fructicola* and *Monilinia laxa* are the primary species responsible for the disease, with *M. fructicola* becoming dominant in the Ebro Valley, a major peach production area in Spain. The fruit cuticle serves as the first line of defense against external threats and may play a key role in determining susceptibility to *Monilinia* spp. This study investigated the influence of fruit cuticular components (both cuticular waxes and cutin) on the susceptibility to *M. fructicola* in 21 Spanish *P. persica* cultivars, with a variable susceptibility to *Monilinia* spp., from the National Peach Collection at CITA (Zaragoza, Spain). The results indicate that both cuticular waxes and the cutin matrix significantly influence fruit susceptibility to *M. fructicola*. Specifically, several cuticular wax compounds, including pentacyclic triterpenoids and very-long-chain alkanols, as well as certain cutin monomers, were strongly negatively correlated with susceptibility to *M. fructicola*. These findings underscore the crucial role of cuticular components in fruit defense against *M. fructicola* and suggests that introgression of these traits could help breed cultivars with reduced susceptibility to *Monilinia* spp.

1. Introduction

Brown rot, caused by the fungus *Monilinia* spp., is one of the most economically important diseases in stone fruits worldwide (Byrde and Willetts, 1977; van Leeuwen et al., 2002; Holb, 2019). In Spain, *Monilinia laxa* and *Monilinia fructicola* have been the most recurrent pathogens since the dislodgement of *Monilinia fructigena* in 2010 (Villarino et al., 2013). Similar to what has also been reported in Californian *Prunus persica* (peach) orchards during the second half of the twentieth century (Hewitt and Leach, 1939; Zehr, 1982; Ogawa et al. 1984), *M. fructicola* is nowadays the predominant *Monilinia* spp. in the Ebro Valley, one of the main *P. persica* growing areas in Spain. The *Monilinia* spp. infection probably cause over 60 % of post-harvest fruit loss (Villarino et al., 2016; Obi et al., 2019), which represents huge food waste and economical losses for the growers.

Although most commercial *P. persica* cultivars are sensitive to *Monilinia* spp., some degree of tolerance to *Monilinia* spp. has been reported in the Brazilian landrace cultivar 'Bolinha' (Feliciano, 1987) and some advanced selections from the University of California (Martínez-García et al., 2013). Although the resistance in 'Bolinha' has mainly been attributed to its fruit cuticle (Gradziel and Wang, 1993), the exact mechanisms of tolerance remain unclear.

High levels of phenols and polyphenol oxidase enzyme activity in the fruit flesh have been associated with lower susceptibility to *Monilinia* spp. (Gradziel and Wang, 1993; Gradziel et al., 2002; Villarino et al., 2011). In studies of various *Prunus* species, infection rates were more variable in uninjured fruits than in artificially injured fruits, suggesting a defensive role of the fruit cuticle (Pascal et al., 1994; Martínez-García et al., 2013; Pacheco et al., 2014; Fu et al., 2018; Fu et al., 2022). Recent research has shown that *P. persica* fruits with a thicker or denser cuticular layer are more resistant to infection (Martínez-García et al., 2023; Gradziel et al., 2002; Oliveira Lino et al., 2016).

The cuticle also acts as a mechanical and dynamic barrier during plant-pathogen interactions, containing anti-pathogenic compounds such as terpenoids and flavonoids (Reina-Pinto and Yephremov, 2009; Ziv et al., 2018). However, little information is available about the cuticular components in *P. persica* and their defense role against pathogenic infections. Recent studies have characterized the cuticle composition in different cultivars and its relation to susceptibility to *Monilinia* spp. (Oliveira-Lino et al., 2022; Mustafa et al., 2024).

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In this context, the objectives of this study were to (a) characterize the cuticular waxes and cutin matrix profile in fruit from 21 Spanish *P. persica* cultivars with varying susceptibility to *M. fructicola*; and, (b) investigate the potential relationship between cuticular components and fruit susceptibility to *M. fructicola* infection.

2. Materials and methods

2.1. Plant material

A total of 21 Spanish accessions (2 trees per cultivar) of *P. persica* (L.) Batsch (peach) from the National peach collection at Centro de Investigación y Tecnología Agroalimentaria de Aragón (CITA) were studied during the harvest season 2019 (Table 1). The 21 Spanish *P. persica* cultivars were selected according to data of our previous study (Martínez-García et al., 2023) in order to have a wide range of susceptibility to *M. fructicola*. The CITA peach collection was established in 2010 in Zaragoza, North Eastern Spain (latitude 41 43 42.7 N, longitude 0 48 44.1 W), grafted onto the hybrid rootstock 'Garnem' of *P. persica* and *Prunus dulcis* (almond). Standard cultural practices, including pruning and fruit thinning and chemical spray programs were followed. However, no fungicidal treatments against *Monilinia* spp. were applied after flowering time.

Table 1
List of 21 Spanish *Prunus persica* cultivars used in this study, their region of origin and their main fruit attributes and their harvest season.

Cultivar Name	Region of origin	Fruit Type	Flesh color	Flesh type	Harvest season*
Blanco Tardío	Zaragoza	Peach	White	Melting	Late
Calabacero Deleite	Murcia	Peach	Yellow	Non-melting	Mid
Calabacero Soto	Murcia	Peach	Yellow	Non-melting	Mid
Fraga	Huesca	Peach	White	Non-melting	Late
Gallur	Zaragoza	Peach	Yellow	Non-melting	Late
Jeronimo	Murcia	Peach	Yellow	Non-melting	Mid
La Escola	Lérida	Peach	Yellow	Non-melting	Mid
Miraflores	Zaragoza	Peach	Yellow	Non-melting	Late
Miraflores Serapio	Zaragoza	Peach	Yellow	Non-melting	Late
Montaced	Huesca	Peach	White	Non-melting	Late
Paraguayo Almudi	Zaragoza	Flat	White	Melting	Mid
Paraguayo Almunia	Zaragoza	Flat	White	Melting	Mid
Pigat	Huesca	Peach	Yellow	Non-melting	Late
Pomar	Huesca	Peach	White	Non-melting	Late
Rojo de Tudela	Navarra	Peach	Yellow	Non-melting	Late
Rojo del Rito	Lérida	Peach	Yellow	Non-melting	Late
San Lorenzo	Huesca	Peach	Yellow	Non-melting	Mid
Sudanell 1	Lérida	Peach	Yellow	Non-melting	Late
Sudanell 2	Lérida	Peach	Yellow	Non-melting	Late
Valentin	Navarra	Peach	White	Non-melting	Late
Villamayor	Zaragoza	Peach	White	Non-melting	Late

* Harvest season as mid (from 15th July to 15th August) and late (from 15th August).

2.2. Susceptibility to M. fructicola

The fruits from each tree were harvested at commercial maturity (according to fruit color and fruit flesh firmness) and immediately transported to the laboratory for the assays. From the fruit collected per tree on each harvest date, twenty unblemished fruits of similar maturity determined by index of absorbance difference (I_{AD}; Ziosi et al., 2008) were used for inoculations. Fruit susceptibility to *M. fructicola* (Winter) Honey infection was evaluated by controlled inoculation on non-wounded fruit following the protocol described in Martínez-García et al. (2023). The strain of *M. fructicola* used in this study (CPMC3) was provided by the Postharvest Pathology group of IRTA (Lleida, Catalonia, Spain) and was isolated from a latent infection of a *P. persica* fruit from a commercial orchard. Twenty non-wounded fruits of each tree (two trees per cultivar) were inoculated by adding a 10 μL droplet of inoculum with the concentration of 10^5 conidia per mL of *M. fructicola* isolate CPMC3. Perpendicular *M. fructicola* lesion diameter or brown rot diameter (BRD) was recorded five days after inoculation and incubation of the *P. persica* in the dark humidified containers at 20 °C ± 1 °C. When the BRD exceeded 70 mm, a maximum BRD of 70 mm was assigned. Disease severity index (DSI) for each cultivar was calculated as the product of the BRD mean value and the proportion of fruit with lesions exceeding 10 mm as disease incidence, following the protocol of Fu et al. (2018) with modifications, and averaged for two trees per cultivar.

2.3. Cuticle isolation

For fruit cuticle assays, three unblemished fruits per tree (and two trees per cultivar) were selected, and five epidermal disks with a diameter of 13 mm were cut with a cork borer from the equatorial part of each fruit (Fig. 1). Maximum amount of fruit flesh was manually removed from each disk, and then the fruit cuticles were isolated enzymatically by incubation in pectinase and cellulase buffer, following the protocols of Belge et al. (2014). Isolated fruit cuticles were dried at room temperature for 24 h and then stored until analysis.

2.4. Cuticle area density and thickness

Cuticle area density (from now on, just density) and thickness were analyzed as described in Martínez-García et al. (2023) (Fig. 2). Isolated fruit cuticles were gravimetrically weighed for cuticle density calculation. For microscopic examination (Fig. 2), 2 mm thick fruit surface pieces were fixed, dehydrated and embedded in paraffin following the protocol of Alcaraz et al. (2013). Transverse sections were cut with a microtome, stained with Sudan IV and then examined by microscopy. Software ImageJ (version 1.47r) was used to calculate cuticle thickness using microscopic images. In each microscopic image, the mean value of the cross section of five points across the cuticle was obtained avoiding areas with trichomes.

2.5. Cuticular wax analysis

For cuticular wax analysis, three isolated fruit cuticles from each tree were used (two trees per cultivar) (Fig. 1). Cuticular waxes were extracted successively by immersing the isolated fruit cuticles at room temperature in trichloromethane (Roth) for 2 h and twice in methanol (Roth) for 15 s. *N*-tetracosane (Fluka) was added as internal standard, and the organic solvent was evaporated under a gentle flow of nitrogen. Cuticular waxes were derivatized for gas chromatography with *N,O*-bis (trimethylsilyl)trifluoroacetamide (Marchery-Nagel) in anhydrous pyridine (Merck) at 60 °C for 60 min. Quantification of cuticular waxes was performed with a gas chromatograph equipped with a flame ionization detector and an on-column injector (7890A, Agilent Technologies). Separation of cuticular wax compounds was carried out on a fused-silica capillary column (DB1-ms, 30 m length × 0.32 mm internal diameter, 0.1 μm film, Agilent Technologies) with hydrogen as carrier gas. The gas

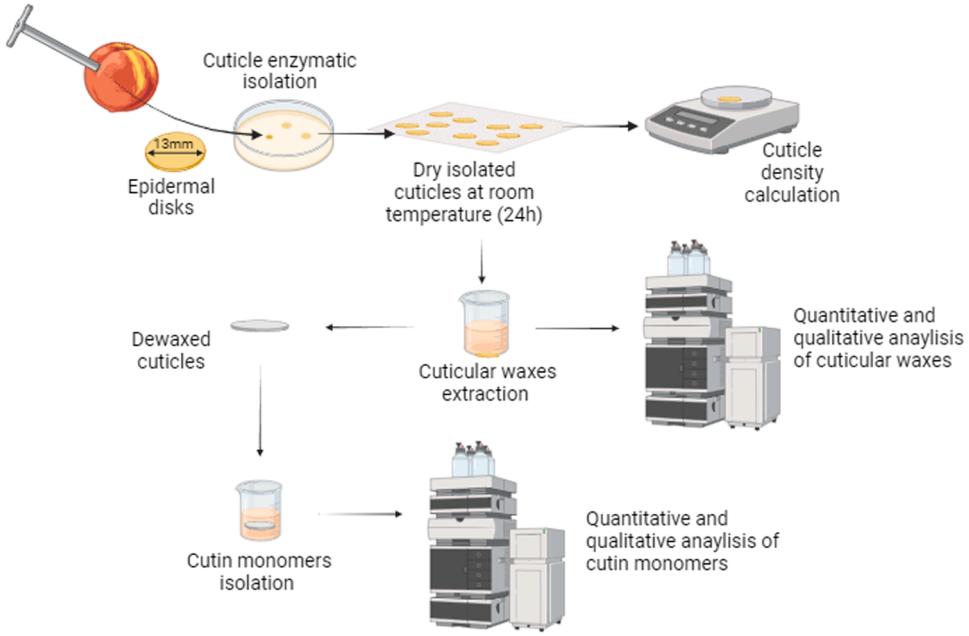


Fig. 1. Methodological graphic to summarize the protocols for cuticle isolation, cuticle area density measurement, and cuticular wax cutin monomers quantitative and qualitative analysis. Graphic made with the free version of BioRender.

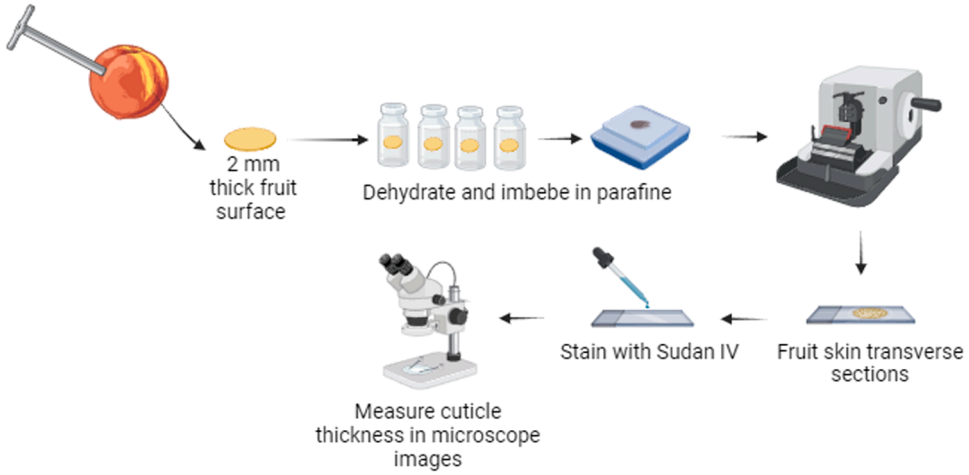


Fig. 2. Methodological graphic to summarize the protocols used to measure cuticle thickness. Graphic made with the free version of BioRender.

inlet pressure was programmed at 50 kPa for 5 min, by 3 kPa min^{-1} to 150 kPa, and at 150 kPa for 40 min. The temperature program started with injection at 50 °C for 2 min, raised by 40 °C min^{-1} to 200 °C, held at 200 °C for 2 min, then raised by 3 °C min^{-1} to 320 °C, and, finally, held at 320 °C for 30 min.

Single cuticular wax compounds were quantified against the internal standard and were calculated per unit of fruit surface area. Qualitative cuticular wax analysis was carried out using a gas chromatograph equipped with a mass spectrometric detector (5977A MSD, Agilent Technologies) following the same gas chromatographic conditions, except that helium was the carrier gas. Cuticular waxes were identified by the electron ionization-mass spectra.

2.6. Cutin analysis

For the analysis of cutin monomers, three isolated fruit cuticles from each tree were used (two trees per cultivar) (Fig. 1). Cutin monomers were obtained from dewaxed fruit cuticles through double transesterification with boron trifluoride in methanol (Sigma-Aldrich) overnight at 70 °C. After cooling, trichloromethane (v/v; Roth) as solvent and *n*-dotriacontane (Sigma-Aldrich) as internal standard were added to the extracts. The trans-methylated cutin monomers were washed three times with sodium-chloride saturated aqueous solution, were dried with anhydrous sodium sulphate (AppliChem) and filtered. Subsequently, the organic solvent was evaporated under a gentle flow of nitrogen.

Derivatization and gas chromatographic analysis were performed according to the cuticular wax analysis with the same equipment. Separation of cutin monomers was carried out at 50 kPa for 60 min, by 10 kPa min^{-1} to 150 kPa, and at 150 kPa for 30 min. The gas chromatographic conditions consisted of injection at 50 °C for 1 min, raised by 10 °C min^{-1} to 150 °C, held at 150 °C for 2 min, raised by 3 °C min^{-1} to 300 °C, and, finally, held at this temperature for 30 min.

2.7. Statistical analysis

Statistical analyses were carried out by SPSS Statistics (SPSS Statistics 29.0.0.0; IBM®). Normality of the datasets was tested by Shapiro-Wilk test with a p-value threshold of 0.05. Correlation analysis among the datasets was performed using Spearmańs rank correlation coefficients at $p < 0.05$.

3. Results and discussion

3.1. Fruit susceptibility to M. fructicola

Fruit susceptibility to *M. fructicola* of the 21 Spanish *P. persica* cultivars, assessed under laboratory conditions on non-wounded fruits in order to keep the natural resistance to infection associated with fruit cuticle, exhibited considerable variability (Fig. 3). Lesion diameter (BRD) after five days of inoculation ranged from 5.91 mm to 69.38 mm, while the disease severity index (DSI) ranged from 1.35 to 69.38. These values align with those reported in previous studies on non-wounded fruits using similar protocols, including the same incubation period and inoculum concentration (Pacheco et al., 2014; Baró-Montel et al., 2019). However, higher DSI values were observed in this study compared to those reported by Fu et al. (2021). This discrepancy may be due to differences in the virulence of the *M. fructicola* strain used, as well as small variations in factors such as temperature and humidity in the infection protocol.

Among the 21 *P. persica* cultivars, ten exhibited DSI values lower than 20 and were classified as low to medium susceptibility to infection, while the remaining eleven cultivars showed DSI values greater than 30 and were considered highly susceptible to *M. fructicola*.

The *P. persica* cultivars with higher fruit susceptibility (higher BRD and DSI) were the three melting cultivars included in this study: two white melting, flat cultivars ‘Paraguayo Almudí’ and ‘Paraguayo Almunia’ and the white melting, late cultivar ‘Blanco Tardío’. Contrary, the lowest susceptibility to *M. fructicola* was shown by two yellow melting cultivars ‘San Lorenzo’ and ‘La Escola’, followed by a white non-melting cultivar ‘Montaced’. The wide variability in susceptibility to *Monilinia* spp. observed among the 21 *P. persica* cultivars provided an opportunity to explore the factors behind these differences, particularly in relation to the structure and composition of the fruit cuticle.

3.2. Cuticle thickness and cuticle area density

The cuticle thickness of the 21 *P. persica* cultivars in this study ranged from 5.50 μm in the yellow non-melting cultivar ‘Calabacero Soto’ to 7.93 μm in the yellow non-melting cultivar ‘San Lorenzo’ (Fig. 4). To our knowledge, no previous data have been reported on cuticle thickness analysis across such a wide range of *P. persica* cultivars. The variation in cuticle thickness has been linked to various ecological strategies in different plant organs. In leaves, for example, thicker cuticles have been associated with higher mechanical resistance (Alonso-Forn et al., 2023).

Additionally, the cuticle area density ranged from 15.37 μg mm^2 in the yellow non-melting cultivar ‘Calabacero Deleite’ to 63.40 μg mm^2 in ‘San Lorenzo’ (Fig. 4), demonstrating substantial variability in fruit cuticle density across different cultivars. While previous reports on this topic are limited, the values obtained in this study fall within the range reported by Belge et al. (2014) for the melting cultivar ‘October Sun’ and the non-melting cultivar ‘Jesca’ (15 μg mm^2 and 13 μg mm^2, respectively). However, some cultivars in this study, such as ‘San Lorenzo’, ‘Paraguayo Almunia’, and ‘Montaced’, exhibited cuticle densities two to three times higher than those reported by Belge et al. (2014). According to Onoda et al. (2012), cuticle density in leaves is associated with mechanical resistance, a relationship that could potentially extend to fruit cuticles in terms of defense against pathogens. Despite the observed variability in cuticle surface density among the *P. persica* cultivars, no clear relationship was found between cuticle density and susceptibility to pathogenic attack. For instance, the yellow non-melting peach ‘San Lorenzo’ and the white melting flat peach ‘Paraguayo Almunia’ exhibited similar fruit cuticle densities, yet they showed opposite extremes in susceptibility to *Monilinia* spp. This highlights the complexity of the interaction between cuticle characteristics and disease resistance, suggesting that further studies are necessary to investigate the role of cuticle features in other aspects of fruit defense, such as resistance to mechanical damage.

These results demonstrate, in line with previous studies (Gradziel and Wang, 1993; Pacheco et al., 2014; Oliveira-Lino et al., 2016, 2022; Martínez-García et al., 2023; Mustafa et al., 2023), the importance of the fruit cuticle as the first line of defense against various pathogens. Additionally, we demonstrate the critical role of the fruit cuticle structure in defending *P. persica* against *Monilinia* spp. infection, a finding consistent with studies on other fungi affecting *Malus domestica* (apple; Konarska, 2012), *Vaccinium macrocarpon* (cranberries; Özgen et al., 2002), *Vitis vinifera* (grape; Marois et al., 1985; Gabler et al., 2003), and *Hylocereus undatus* (pitaya; Huang et al., 2024).

3.3. Fruit cuticle composition

The plant cuticle is a hydrophobic coating primarily composed of a cutin matrix, polymerized by hydroxylated, epoxy hydroxylated, and dicarboxylic alkanoic acids, along with embedded cuticular waxes. These components play a key role in controlling transpiration and preventing invasions by pathogens and insects (Fernández-Muñoz et al., 2022; Huang et al., 2023; Huang et al., 2024). Both the cutin matrix and cuticular waxes (Bessire et al., 2007; Reina-Pinto and Yephremov, 2009) are essential for plant defense. Despite their recognized importance, few studies have analyzed the impact of cuticular composition on fruit susceptibility to pathogens, and those that do often report contradictory findings (Oliveira Lino et al., 2020; Mustafa et al., 2023; Huang et al., 2024).

3.3.1. Cuticular wax composition

A wide variability in cuticular wax loads was observed among the 21 *P. persica* cultivars, ranging from 226 μg cm^2 in the non-melting cultivar ‘Rojo del Rito’ to 450 μg cm^2 in the non-melting cultivar ‘Gallur’ (Fig. 5 and Sup. Figure 1). Higher cuticular wax loads were detected in yellow non-melting cultivars like ‘Gallur’ (450 μg cm^2) and ‘Rojo de Tudela’ (416 μg cm^2), both of which exhibited low susceptibility to *M. fructicola*. In contrast, the lowest wax loads were found in cultivars such as ‘Pomar’ (224 μg cm^2) and ‘Jerónimo’ (226 μg cm^2), which were more susceptible to the pathogen. The total cuticular wax loads in this study were consistent with those reported by Belge et al. (2014) for two *P. persica* cultivars (426 μg cm^2 and 518 μg cm^2), but were notably higher than the 31 μg cm^2 to 42 μg cm^2 observed for *P. persica* nectarines in Oliveira-Lino et al. (2022).

As in other studies, the cuticular waxes in *P. persica* were found to be complex mixtures of lipids, predominantly consisting of pentacyclic triterpenoids, sterols, flavonoids, tocopherols, and very-long-chain aliphatic compounds such as alkanoic acids, n-alkanes, alkanals, alkanones, and alkanols (Yeats and Rose, 2013; Lara et al., 2015; Oliveira-Lino et al., 2022). In this work, 15 compound classes were identified (Table 2). These include five main compound classes of very-long-chain aliphatic waxes: n-alkanes, alkanals, alkanoic acids, primary alkanols, and alkyl esters; two sterols: β-sitosterol and stigmasterol; and eight pentacyclic triterpenoids: oleanoic acid, hederagenin, maslinic acid, α-amyrin, uvaol, ursolic acid, corosolic acid, and derivatives of ursolic acid.

The cuticular wax composition of the peach cultivars was dominated by pentacyclic triterpenoids, which accouned for 36 % to 61 % of total waxes in 11 cultivars (Fig. 5). In contrast, very-long-chain aliphatic waxes were more abundant in 9 cultivars, comprising 38 % to 68 % of the total cuticular wax load. Sterols were the least abundant, making up only 0.4 % to 4 % of the total waxes. The variability in cuticular wax

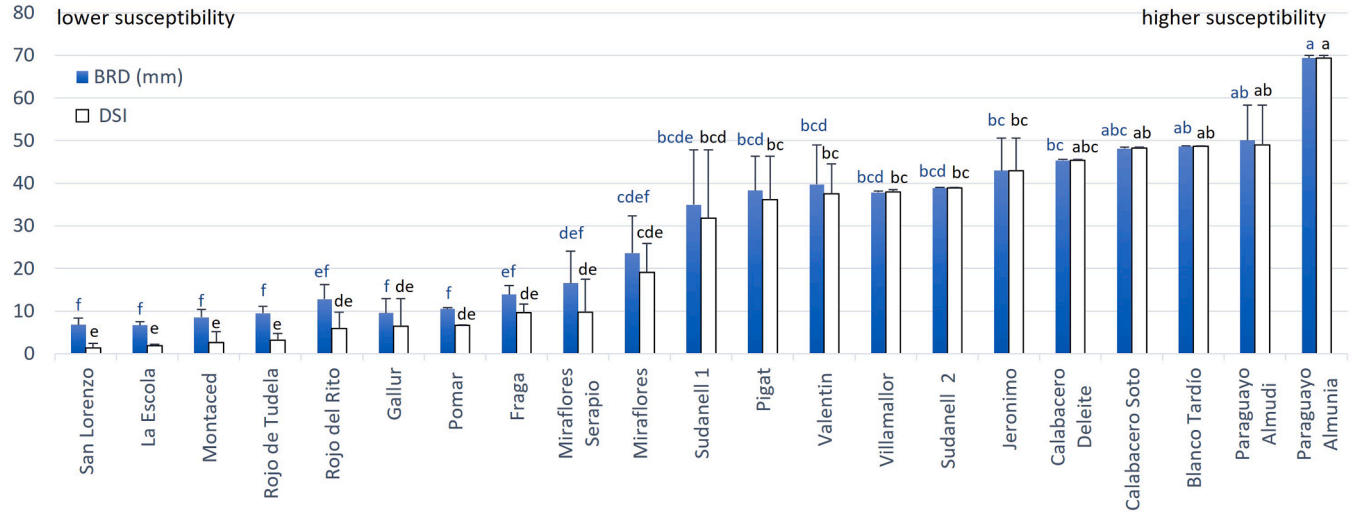


Fig. 3. Disease severity index (DSI) and lesion diameter (BRD) of fruits from 21 Spanish *Prunus persica* cultivars, ordered from lower to higher degree of susceptibility to *Monilinia fructicola*. Mean value and standard deviation of two trees per cultivar are shown. Different letters above the columns for each parameter (DSI and BRD) indicate significant differences among cultivars, as determined by Duncan test at the 0.01 level.

Table 2
List of cuticular components (cuticular waxes and cutin matrix) identified and quantified in the fruits from 21 Spanish *Prunus persica* cultivars.

Cuticular waxes		Cutin monomers	
Very-long-chain aliphatic compounds	n-alkanes	Alkanols and alkanoid acids	primary alkanols
	alkanals		alkanoic acids
	alkanoic acids		ω-hydroxy alkanoic acids
	primary alkanols		9/10,ω-dihydroxy alkanoic acids
	alkyl esters		9,10-epoxy ω-hydroxy alkanoic acids
Sterols	β-sitosterol		9,10,ω-trihydroxy alkanoic acids
	stigmasterol	α,ω-dicarboxylic acids	α,ω-dicarboxylic acid
Pentacyclic triterpenoids	oleanolic acid		9/10-hydroxy α,ω-dicarboxylic acid
	hederagenin		9,10-epoxy α,ω-dicarboxylic acid
	maslinic acid	Hydroxy cinnamic acids	o-coumaric acid
	α-amyrin		p-coumaric acid
	uvaol		ferulic acid
	ursolic acid		caffeic acid
	corosolic acid		
	ursolic acid derivatives		

composition observed in this study is consistent with previous findings on wax variability within and among plant species (Belge et al., 2014; Oliveira-Lino et al., 2022; Huang et al., 2024). Such variability can arise from differences in growth and developmental stages of plant organs (Peschel et al., 2007; Diarte et al., 2021) as well as from environmental factors (Belge et al., 2014). The predominance of pentacyclic triterpenoid acids in the intracuticular wax layer of peach fruit (Vogg et al., 2004; Wang et al., 2014) is consistent with previous reports for *P. persica* cultivars, including 'October Sun' (52 %) and 'Jesca' (44 %) (Belge et al., 2014). These results align with those reported by Belge et al. (2014) for the melting *P. persica* cultivar 'October Sun' (52 %) and the non-melting cultivar 'Jesca' (44 %), although they are lower than the 85 % reported by Oliveira-Lino et al. (2022) for fruits of *P. persica* (nectarine).

Within the very-long-chain aliphatic waxes, n-alkanes were the most abundant compounds, accounting for 17 % to 60 % of this wax fraction, followed by alkyl esters (10 % to 21 %), primary alkanols (7 % to 16 %), alkanoic acids (6 % to 14 %), and alkanals (3 % to 12 %) (Fig. 6). The variability in very-long-chain aliphatic wax coverage ranged from 105.98 μg cm^2 for the white melting cultivar 'Blanco Tardío' to 188.42 μg cm^2 for the white non-melting cultivar 'Montaced'. This variability was primarily attributed to differing levels of n-alkanes, which ranged from 28.24 μg cm^2 to 105.27 μg cm^2 across the cultivars. The n-alkanes accounted for 8 % to 28 % of total cuticular waxes in the peach cultivars studied, which falls within the range reported for the non-melting peach cultivar 'Jesca' (26 %) and the melting peach cultivar 'October Sun' (16 %), as well as for nectarine cultivars 'Summergrand' and 'Zéphir' (9 %; Oliveira-Lino et al., 2022). However, these levels were considerably lower than those observed in the yellow non-melting peach cultivar 'Calanda', which exhibited an n-alkane content as high as 76 % (Fernández et al., 2011).

In terms of pentacyclic triterpenoid coverage, high variability was observed, ranging from 93.38 μg cm^2 in the white non-melting cultivar 'Villamayor' to 269.57 μg cm^2 in the yellow non-melting cultivar 'Gallur' (Fig. 7). Ursolic acid was the most abundant pentacyclic triterpenoid, accounting for 19 % to 70 % of the pentacyclic triterpenoid coverage (66.69 ± 23.93 μg cm^2), followed by oleanolic acid (39.44 ± 13.29 μg cm^2), which contributed 10 % to 34 % of the pentacyclic triterpenoid coverage. These two compounds made up a significant portion of the total wax composition, accounting for 10 % to 37 % of total waxes for ursolic acid and 6 % to 18 % for oleanolic acid. The dominance of ursolic acid and oleanoic acids among pentacyclic triterpenoids agrees to previous results reported for other *P. persica* cultivars (Belge et al., 2014; Belge et al., 2019) and other *Prunus* spp. fruits (Peschel et al., 2007; Lara et al., 2015).

Additionally, a considerable amount of ursolic acid derivatives were detected in the cuticular waxes, accounting for 4 % to 22 % of the pentacyclic triterpenoid coverage, as previously reported in fruits of *P. persica* (nectarine; El Lahloul et al., 1999; Oliveira-Lino et al., 2022).

Other pentacyclic triterpenoids, such as hederagenin, maslinic acid, α-amyrin, uvaol, and corosolic acid, were also identified, albeit in much smaller quantities. These compounds have previously been identified in the hulls of *Prunus dulcis* (almond; Amico et al., 2006) and fruits of *P. persica* (nectarine; Oliveira-Lino et al., 2022). However, this study marks the first time, to our knowledge, that some free pentacyclic triterpenoid acids—specifically hederagenin, α-amyrin, and uvaol—have

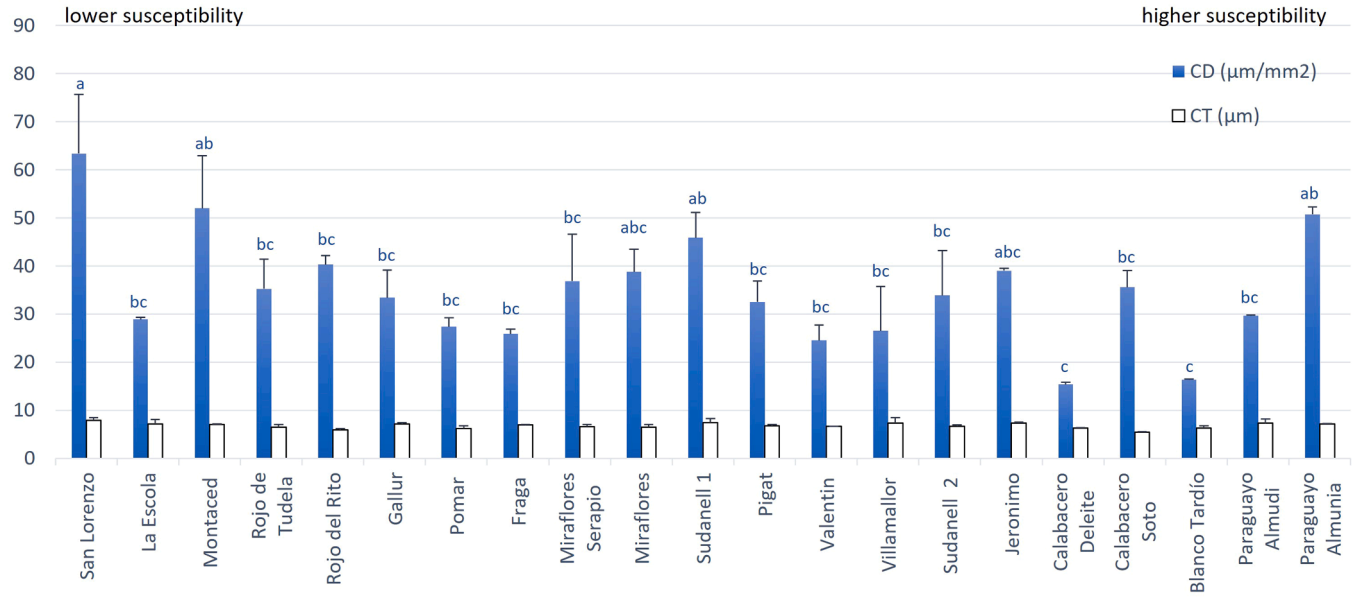


Fig. 4. Cuticle surface density (CD) and cuticle thickness (CT) of fruits from 21 Spanish *Prunus persica* cultivars, ordered from lower to higher degree of susceptibility to *Monilinia fructicola*. Mean value and standard deviation of two trees per cultivar are shown. Different letters indicate significant differences among cultivars for CD, as determined by Duncan test at the 0.01 level.

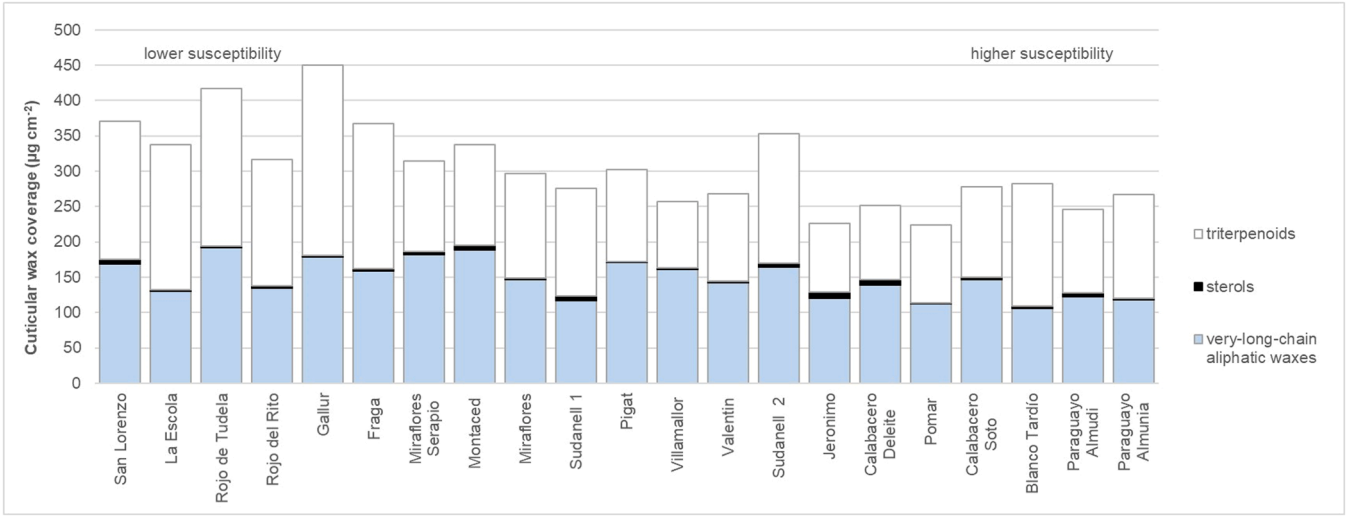


Fig. 5. Cuticular wax composition of fruits from 21 Spanish *Prunus persica* cultivars ordered from lower to higher degree of susceptibility to *Monilinia fructicola*.

been identified in the cuticular waxes of *P. persica* fruits. Notably, these same compounds have also been reported in the cuticles of *Prunus avium* (sweet cherry; Peschel et al., 2007) and in the evergreen model plant *Prunus laurocerasus* drupes (Diarte et al., 2021). This highlights the widespread presence of these triterpenoids across various *Prunus* species, suggesting their potential significance in plant defense and cuticular wax composition.

The sterol content in the cuticular waxes also showed considerable variability, ranging from 1.17 µg cm^2 in the yellow non-melting cultivar 'Pigat' to 9.16 µg cm^2 in 'Jerónimo' (Fig. 8). The sterols detected included stigmasterol (1.41 ± 1.00 µg cm^2) and β-sitosterol (2.46 ± 1.35 µg cm^2), with β-sitosterol being the most abundant sterol in most cultivars. Interestingly, campesterol was not detected in this study, despite being previously identified as the most abundant sterol in *P. persica* cultivars such as 'Jesca' and 'October Sun' (Belge et al., 2014) .

3.3.2. Cutin composition

Regarding the cutin matrix, 15 different cutin monomers were identified belonging to aliphatic and aromatic compound classes: alkanols and alkanoic acids, α,ω-dicarboxylic acids, and hydroxy cinnamic acids (o-coumaric acid, p-coumaric acid, ferulic acid and caffeic acid) (Table 2).

Cutin load varied significantly among the 21 *P. persica* cultivars, ranging from 138.71 µg cm^2 for the white non-melting cultivar 'Villamayor' to 410.73 µg cm^2 for the yellow non-melting cultivar 'Gallur' (Fig. 9 and Sup. Figure 2). Higher cutin loads were generally observed in cultivars with lower susceptibility to *M. fructicola*. The main cutin monomers identified were 9,10-epoxy ω-hydroxy alkanoic acids, which accounted for 11 % to 55 % of total cutin monomers, followed by 9/10,ω-dihydroxy alkanoic acids (14 % to 38 %), 9,10,ω-trihydroxy alkanoic acids (14 % to 35 %), and ω-hydroxy alkanoic acids (4 % to 12 %). Primary alkanols, α,ω-dicarboxylic acids, and hydroxy cinnamic acids were also detected, though in much smaller quantities. This variation in

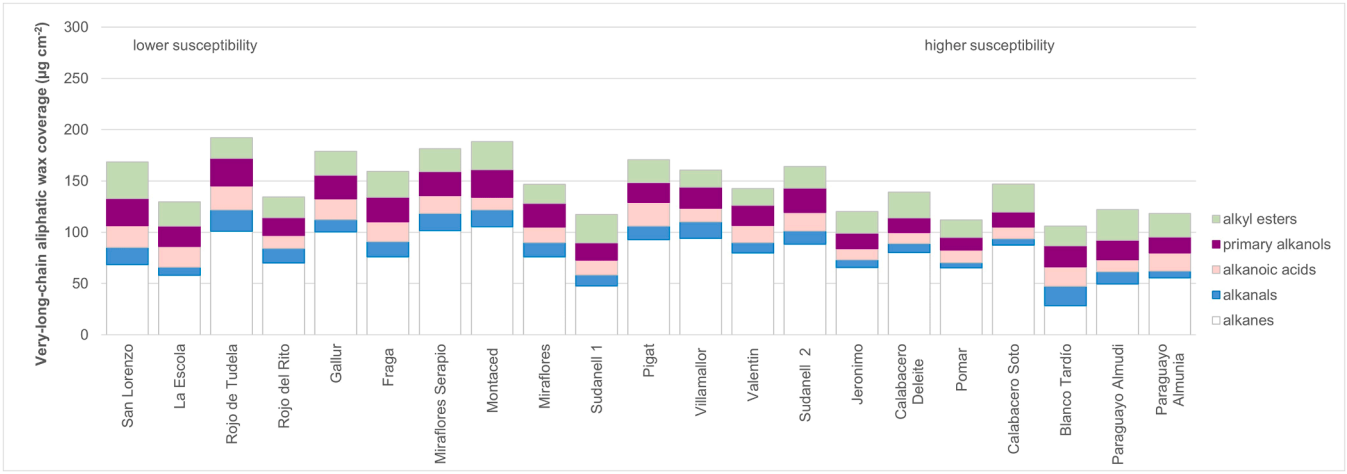


Fig. 6. Very-long chain aliphatic wax coverage of the fruit cuticle from 21 Spanish *Prunus persica* cultivars ordered from lower to higher degree of susceptibility to *Monilinia fructicola*.

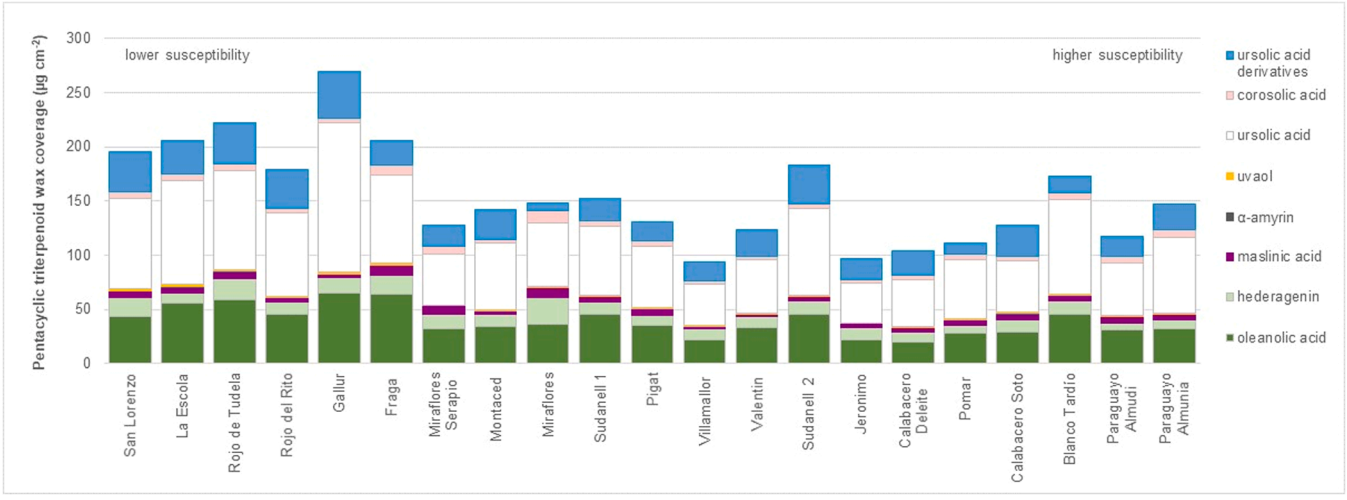


Fig. 7. Pentacyclic triterpenoid wax coverage of the fruit cuticle from 21 Spanish *Prunus persica* cultivars ordered from lower to higher degree of susceptibility to *Monilinia fructicola*.

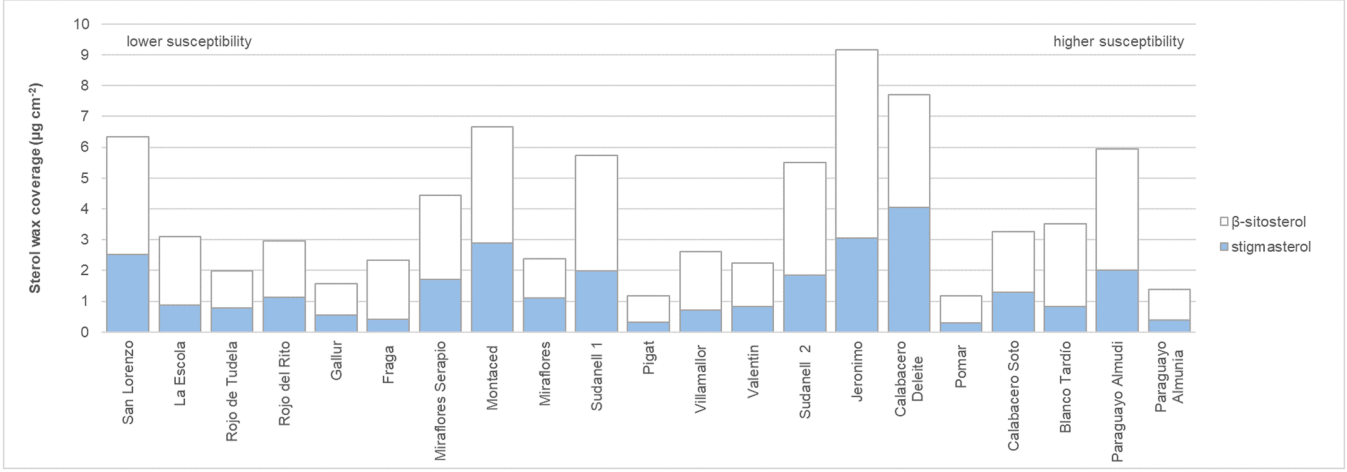


Fig. 8. Sterol wax coverage of the fruit cuticle from 21 Spanish *Prunus persica* cultivars ordered from lower to higher degree of susceptibility to *Monilinia fructicola*.

total cutin load and the relative abundance of each cutin monomer has been observed in previous studies on peach (Lara et al., 2014; Belge et al., 2014; Oliveira-Lino et al., 2022). According to Dominguez et al. (2011), differences in monomeric composition can play a crucial role in the cuticle's physical properties and, consequently, its protective function against pathogens.

3.4. Correlations between cuticle composition and susceptibility to *M. fructicola*

To investigate the potential contribution of the cuticular composition of P. persica fruits to susceptibility to M. fructicola, we analyzed the relationships between infection severity (DSI) and lesion diameter (BRD) with the amount of the cuticular components. Both cuticular wax and cutin loads showed significant negative correlations with fruit susceptibility to M. fructicola (Table 3), indicating the role of both cuticular components in defense against infection, as previously reported by Oliveira-Lino et al. (2022). The correlation between DSI and cuticular wax load was stronger than that with cutin load (-0.75 vs. -0.58), suggesting that cuticular waxes play a more significant role in fruit defense against M. fructicola.

Among the identified cuticular waxes, only the quantity of primary alkanols and pentacyclic triterpenoids showed significant negative correlations with DSI and BRD, suggesting that these cuticular wax compounds may play a role in fruit defense against *M. fructicola*. Five different pentacyclic triterpenoids exhibited significant negative correlations with DSI and BRD. Oleanoic acid showed the highest correlation (r^2 = -0.64, $p < 0.01$), followed by uvaol (r^2 = -0.57, $p < 0.01$), hederagenin (r^2 = -0.55, $p < 0.05$), ursolic acid (r^2 = -0.52, $p < 0.05$), and ursolic acid derivatives (r^2 = -0.50, $p < 0.05$). These results indicate that higher quantity of these cuticular compounds correlate with lower susceptibility to infection. In line with these findings, other studies have linked higher tolerance to *Monilinia* spp. in certain *P. persica* cultivars to greater amounts of epicuticular waxes (Gradziel and Wang, 1993; Crisosto et al., 1997; Gradziel et al., 2002). In a recent study, Oliveira-Lino et al. (2022) demonstrated that pentacyclic triterpenoid deposition during fruit growth in three *P. persica* (nectarine) cultivars, including 'Summergrand' and 'Zéphir', likely plays a major role in regulating fruit permeability and susceptibility to *M. laxa*. The anti-pathogenic activity of oleanolic acid has been previously reported against *B. cinerea* and *Sclerotinia sclerotiorum* (Zhao et al., 2011). Ursolic acid has been considered an active compound against pathogenic attack, as reported by Shu et al. (2019) in a study on black spot rot on *Malus domestica* (apple) fruit induced by *Alternaria alternata*. Oliveira-Lino et al. (2020) found that ursolic acid and oleanolic acid were the most abundant pentacyclic triterpenoids in the *P. persica* (nectarine) fruit cuticle and concluded that there is a clear relationship between the abundance of these compounds and lower susceptibility to *Monilinia* spp. However, despite these findings suggesting a major role of these compounds in the defense of *P. persica* cultivars against *Monilinia* spp., further studies are needed to fully elucidate their role in resistance. In fact, Mustafa et al. (2023) did not find an inhibitory effect in vitro for either ursolic acid or oleanolic acid against *M. laxa* and *M. fructicola*.

On the other hand, no significant correlations were observed between fruit susceptibility to *M. fructicola* and other cuticular wax compounds such as n-alkanes, alkanals, alkanoic acids, alkyl esters, and sterols.

Regarding the cutin matrix, the cutin monomers with the strongest negative correlations with DSI and BRD were α,ω-dicarboxylic acids (r^2 = -0.62, $p < 0.01$), followed by ω-hydroxy alkanoic acids (r^2 = -0.61, $p < 0.01$) and 9/10,ω-dihydroxy alkanoic acids (r^2 = -0.56, $p < 0.01$). No significant correlations with fruit susceptibility to *M. fructicola* were found for primary alkanols, alkanoic acids, and hydroxy cinnamic acids. However, Mustafa et al. (2023) proposed that ferulic acid, a hydroxy cinnamic acid also found in low concentration in the fruit cuticle in this study, might exhibit effective anti-pathogenic activity. According to Hernández et al. (2021), ferulic, p-coumaric acids, and flavonoids (naringin, hesperidin, and neohesperidin) demonstrate in vitro inhibitory effects against *M. fructicola*.

4. Conclusions

This study is the first to characterize the cuticular waxes and cutin monomers in 21 Spanish *Prunus persica* cultivars and their relationship to susceptibility to *Monilinia* spp. infection. The results suggest that the fruit cuticle plays a key role in defending against *Monilinia* spp. No direct link was found between cuticle thickness and pathogen susceptibility, but differences in cuticle surface density were noted, potentially reflecting ecological adaptations for mechanical resistance, although no correlation with pathogen susceptibility was established. Key findings include the negative correlation between pentacyclic triterpenoids and primary alkanols with disease severity, with ursolic and oleanolic acids suggested to enhance resistance, though more research is needed to fully understand their mechanisms.

The study also highlighted the complex nature of cuticular wax composition, with n-alkanes being prevalent but not significantly correlated with pathogen resistance, suggesting that their primary role may be in regulating water loss rather than pathogen defense.

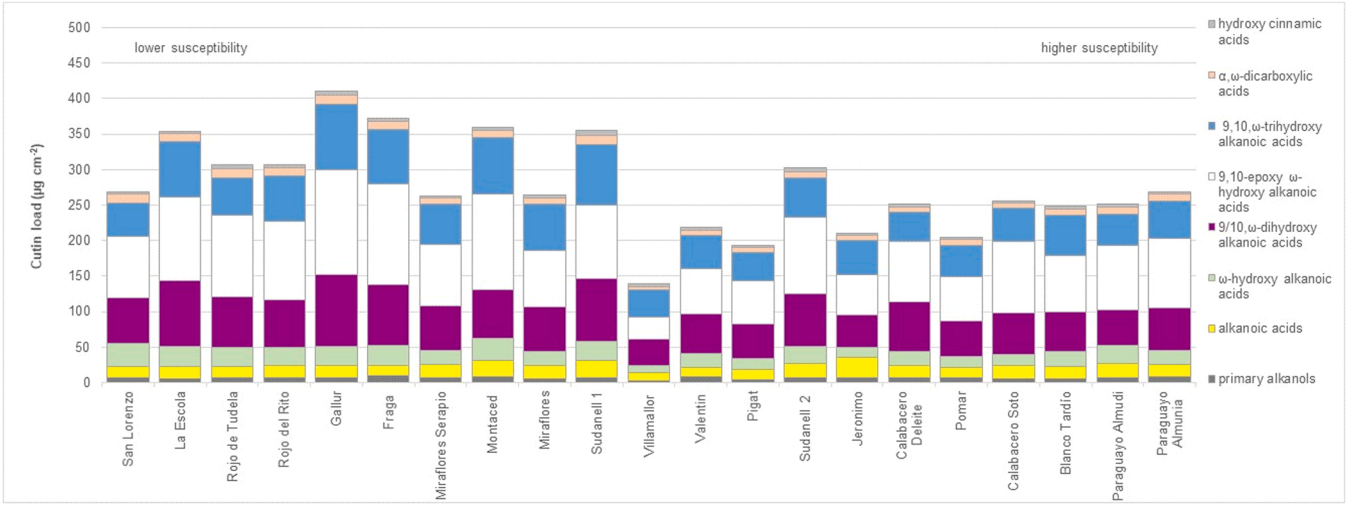


Fig. 9. Cutin monomeric composition of fruits from 21 Spanish *Prunus persica* cultivars ordered from lower to higher degree of susceptibility to *Monilinia fructicola*.

Table 3
Spearman's correlation between cuticular components (cuticular waxes and cutin), susceptibility parameters for *Monilinia fructicola* (lesion diameter [BRD] and disease severity index [DSI]), and cuticular anatomy (cuticle density [CD] and cuticle thickness [CT]) from 21 Spanish *Prunus persica* cultivars. Significant correlations (* at the 0.05 level; ** at the 0.01 level) are highlighted in bold.

		DSI	BRD	CD	CT
cuticular waxes	**cuticular wax load**	**-0,75** **	**-0,62** *	0,19	0,20
	n-alkanes	-0,40	-0,38	-0,20	-0,07
	alkanals	-0,52	-0,35	-0,11	0,10
	alkanoic acids	-0,42	-0,29	0,20	0,25
	primary alkanols	**-0,70** **	**-0,54** *	0,13	0,36
	alkyl esters	-0,18	-0,07	**0,67** **	**0,56** *
	sterols	0,05	0,13	0,14	0,28
	pentacyclic triterpenoids	**-0,64** **	**-0,53** *	0,24	0,15
cutin monomers	**cutin matrix**	**-0,58** **	**-0,49** *	0,24	0,17
	primary alkanols	-0,14	-0,15	0,37	0,16
	alkanoic acids	0,09	0,13	0,08	0,06
	ω-hydroxy alkanoic acids	**-0,61** **	**-0,50** *	0,43	0,38
	9/10,ω-dihydroxy alkanoic acids	**-0,56** **	**-0,48** *	0,23	0,18
	9,10-epoxy ω-hydroxy alkanoic acids	**-0,51** *	-0,42	0,23	0,07
	9,10,ω-trihydroxy alkanoic acids	**-0,54** *	**-0,48** *	0,11	0,20
	α,ω-dicarboxylic acids	**-0,62** **	**-0,55** *	0,42	0,31
	hydroxy cinnamic acids	-0,33	-0,19	0,16	0,12

Sterols	DSI	BRD	CD	CT
β-sitosterol	0,07	0,15	0,17	0,36
stigmasterol	0,02	0,09	0,09	0,15

Pentacyclic triterpenoids	DSI	BRD	CD	CT
oleanolic acid	**-0,64** **	**-0,53** *	0,17	0,14
hederagenin	**-0,55** *	-0,42	0,05	-0,07
maslinic acid	-0,27	-0,23	0,10	-0,04
α-amyrin	-0,10	-0,09	-0,04	0,29
uvaol	**-0,57** **	**-0,50** *	0,11	0,12
ursolic acid	**-0,52** *	**-0,46** *	0,20	0,16
corosolic acid	-0,19	-0,16	0,06	-0,04
derivatives	**-0,50** *	-0,34	0,35	0,16

Furthermore, while the overall wax load, particularly pentacyclic triterpenoids, was correlated with reduced susceptibility to infection, the study underscores the need for additional research to unravel the specific interactions between wax components and pathogen resistance.

However, the study was conducted in Zaragoza, Spain, and may not represent the full spectrum of environmental conditions affecting peach cultivation. Factors such as climate, soil, and orchard management practices could influence cuticular composition and fruit susceptibility, which were not considered in this work.

Future research should include in vitro studies to demonstrate the antifungal capacity of the identified cuticular components, as well as the identification of specific genes responsible for the production of cuticular waxes and cutin monomers associated with resistance. Additionally, understanding the biochemical mechanisms of these compounds could help develop peach cultivars with enhanced resistance to Monilinia, offering valuable implications for breeding strategies in fruit protection.

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CRediT authorship contribution statement

Celia M. Cantín: Investigation, Methodology, Writing – review & editing, Writing – original draft, Supervision, Conceptualization, Funding acquisition, Data curation. **Jana Leide:** Writing – review & editing, Methodology, Investigation, Data curation. **Aline Xavier De Souza:** Writing – review & editing, Methodology, Investigation. **Amauri Bueno:** Methodology, Investigation, Data curation, Writing – review & editing. **Eustaquio Gil:** Writing – review & editing.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Celia M. Cantin reports financial support was provided by Spain Ministry of Science and Innovation and Gobierno de Aragón. Celia M. Cantin reports financial support was provided by State Agency of Research. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.scienta.2025.114341.

Data availability

No data was used for the research described in the article.

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