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ORIGINAL ARTICLE

# Features of the fruit epicuticular waxes of *Prunus persica* cultivars and hybrids concerning pathogens susceptibility

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The high susceptibility of peach (*Prunus persica* L. Batsch) fruits to fungal diseases, which cause significant crop losses and a decrease in crop quality and the unsatisfactory effectiveness of chemical pathogen control agents, force us to look for unrealized reserves of plant resistance. In this regard, we hypothesized that the identification of differences in the hydrocarbon composition of fruit epicuticular waxes of peaches hybrids, which differ in resistance to pathogens, may contribute to a better understanding of the possible role of wax components in pathogenesis. The study was carried based on the Botanical Garden of Oles Honchar Dnipro National University (Dnipro city, Ukraine) using the ripening peach fruits of the "Red Heaven" cultivar and two hybrids with differences in the crossing schemes, fruit ripening rates, and fruit susceptibility to fungal diseases. The chloroform extracts of fruit epicuticular waxes were analyzed by gas chromatography connected to mass-spectrometry. GC/MS assay was performed using Shimadzu GCMS-QP 2020 EI equipped with a capillary column (5% diphenyl/95% dimethyl polysiloxane) and helium carrier gas. Mass Spectrum Library 2014 for GCMS was used to identify the separated compounds of the wax extracts. The dominant components of all peach fruits' epicuticular waxes were *n*-alkanes with an even and odd carbons number from C27 to C60. Of these, some alkanes with an even number of carbons were represented by several isomers. The epicuticular wax of the most stable hybrid 1 contained a significant portion of odd alkanes, including hexacosane, which can be regarded as a factor contributing to cuticle integrity and, thus, counteracting the pathogenic infection development. The epicuticular fruit wax of the "Red Heaven" cultivar contains the highest total amount of alkanes, responsible for fruit sensitivity to pathogenic fungi attacks. In the epicuticular waxes of the most vulnerable hybrid 2, the highest amount of very-long-chain alkanes, the hexadecanoic fatty acid, and fatty aldehyde eicosanal were detected, which together could cause cuticle damage and high susceptibility of fruits to fungal diseases.
**Keywords:** peach; fungal diseases; resistance, epicuticular wax; n-alkane; aldehyde

## Introduction

Stone fruits, including peaches (*Prunus persica* L. Batsch), are among the most massively produced fleshy fruits globally, making up a significant part of many countries' agricultural economy (Lino et al., 2020). The problem is that peaches, mostly eaten fresh, can only last for a few days and are prone to fungal infections. Powdery mildew, one of the primary peach diseases caused by the ascomycete *Podosphaera pannosa*, causes significant damage (Marimon et al., 2020). No less serious threat to *P. armeniaca* L. and *P. persica* in India is posed by phytopathogenic species *Stigmina carpophila* (Lév.) M.B. Ellis, which cause dark brown leaf spots, premature defoliation, and a subsequent decrease in fruit yields by almost 30% (Dar et al., 2017). One of the most common and poorly controlled fungal diseases caused by *Monilinia* spp. is called brown rot and affects stone fruits both during ripening and after harvest, destroying over a quarter of the crop (Lino, 2016). Significant yield losses and product quality declines are difficult to prevent as only a small arsenal of control agents other than chemical treatments, including fungicides, are available (Marimon et al., 2020).

The pathogenic process's initiation and development is mostly determined by the cuticle's properties, which cover the aerial part of plants and is the primary contact of pathogens with the host plant organism. The cuticle is composed of insoluble polyester cutin and the soluble layer of cuticular waxes, mainly comprised of long-chain fatty acids and their derivatives such as aldehydes and alkanes, secondary alcohols, ketones, primary alcohols, and esters (Heredia, 2003). Intracuticular wax is embedded in the cutin polymer, while outer epicuticular wax accumulates on the cuticle's surface (Lee & Suh, 2015). Plant cuticle provides many vital physiological processes, including control fruit development and ripening (Trivedi et al., 2019), protection against the attacks of insects (Rebora et al., 2020), and pathogens (Łaźniewska et al., 2012). The resistance of the fruits to the fungal diseases is determined by many properties of the fruit cuticle, including the content of phenolic compounds and other secondary metabolites, as was found for the fruits of peach (Lino, 2016), barberry (Khromykh et al., 2018a), and Chaenomeles (Khromykh et al., 2018b; Lykholat et al., 2019).

During pathogenesis, the cuticle components are perceived by invading fungi, which can influence the composition of the host plant cuticle and the cell wall and adjust their pathogenesis and virulence (Serrano et al., 2014; Ziv et al., 2018). At an early stage of infection, most phytopathogenic fungi can synthesize hydrolytic enzymes that directly affect the cuticle and play a key role in pathogenic infection (Shen et al., 2017). These enzymes (cutinases, a class of small nonspecific esterases and lipases) hydrolyze cutin polyester and release cutin monomers. Initially, cutin monomers are formed due to cutinase's main activity in fungi spores that reach host plants' surface. Simultaneously, the released cutin monomers can induce host plant defenses and act as molecular patterns associated with damage (Yeats & Rose, 2013). Thus, changes in the cuticle cause a reaction syndrome in the plant organism, leading to an increase in pathogens' resistance. For example, an increase in cuticle permeability in *Arabidopsis* leaves damaged by *Botrytis cinerea* or treated with cutinase positively correlated with an increase in the synthesis of reactive oxygen species and an increase in plant resistance to the pathogen (L'Haridon et al., 2011).

Despite the importance of cutin in the interaction between the pathogen and the host plant, the first surface that infectious agents and pests encounter are crystals of epicuticular wax. According to Yeats and Rose (2013), the cuticle's superficial wax layer provides the lotus effect, facilitating the flushing of spores of the fungal pathogens from the plant's surface before germination. Thus, the structure and composition of the epicuticular waxes are essential in determining phytopathogens' development and their degree of pathogenicity. Rebora et al. (2020) found that waxes' crystal structure determines the micro-roughness and wettability of the surface in different olive varieties and, consequently, the fruit fly's different ability *Bactrocera oleae* to attach to the surface of ripe fruits. In the genotype of peach cultivars resistant and susceptible to powdery mildew, one of the differentially expressed genes was annotated as a protein involved in the biosynthesis of fruit epicuticular wax (Marimon et al., 2020). Such data led to the conclusion (Wu et al., 2018; Lara et al., 2019) that a clear understanding of the accumulation level and composition of fruit epicuticular wax is essential for obtaining better fruit quality, increasing disease resistance, and developing postharvest treatment strategies. It is known (Quilotet al., 2005; Lino, 2016) that significant qualitative differences inherent in the fruits of peaches of different cultivars are determined by their genotypes obtained due to crossing different parental forms. The work aimed to establish the differences in the composition of the hydrocarbon components of the epicuticular waxes of the fruits of a known variety of peach and new hybrid forms, which are characterized by different resistance to pathogens.

## Materials and methods

Plant material was collected, and the epicuticular wax composition was analyzed in July-August 2020. Peach fruits were taken from the trees of species *Prunus persica* (L.) Batsch ("Red Heaven" cultivar) and two hybrid forms planted in the Botanical Garden of OlesHonchar Dnipro National University (Dnipro city, Ukraine). Studied hybrid forms (hybrid I and hybrid II) were created by E.P. Shoferystov et al. in Nikitsky Botanical Garden (National Academy of Agrarian Sciences of Ukraine). The hybridization schemes were different and included different parental forms for hybrid I: [$F_1$ 324-87 (*P. persica* subsp. *nucipersica* × *P. kansuensis*) × free pollination] and hybrid II: [$F_1$ 1004-88 ((*P. persica* subsp. nucipersica × *P. davidiana*) × *P. persica* subsp. *atropurpurea*) × free pollination]. According to long-term observations, the fruits of the "Red Heaven" variety and both hybrids have different ripening rates and differ in the degree of sensitivity to pathogens. The fruits of hybrid I are the most resistant to fungal diseases and are exposed mainly after full ripening. The fruits of hybrid II are quite susceptible to moniliosis, even at an early stage of ripening. The higher resistance of the fruits of hybrid II to powdery mildew, compared with the sensitivity to moniliosis, can be associated with the peculiarities of its genotype, given *P. davidiana* in the crossing scheme. According to the results of Quilot et al. (2004), in experiments on backcrossing between *P. persica* and wild relatives of *P. davidiana*, it was found that alleles of *P. davidiana* were associated with a positive effect on fruit resistance to powdery mildew. The fruits of "Red Heaven" peach variety are also not resistant to pathogens, but more often in the middle of the ripening process.

Peach fruits were harvested from 1–3 trees of each species or hybrid in incomplete ripeness. Plant material was immediately delivered to the laboratory and subjected to extraction of the epicuticular waxes from fruit surface with chloroform following a known approach (Buchhaus et al., 2007). Briefly, each fruit was immersed for 40–50 seconds in the container with chloroform (10–20 mL depending on the fruit size), after which the total extract was filtered into a flask, then chloroform was eliminated using a rotary evaporator.

The capillary gas chromatography connected to mass-spectrometry assay was applied to study epicuticular waxes' composition from the peach fruits' surface. GC/MS analysis of the chloroform wax extracts was performed using Shimadzu GCMS-QP 2020 EI equipped with Rxi®-5ms column (30 m × 0.25 mm, film thickness 0.25 µm) containing 5% diphenyl/95% dimethyl polysiloxane a fixed liquid phase. The column temperature was kept at 50 °C for 5 min, and then programmed temperature gradient increased to 300 °C at a rate of 15 °C per min and kept constant at 300 °C for 10.5 min. The carrier gas helium passed at a flow rate of 54 ml/min. Injector temperature was 300 °C; sample volume was 1 µl. Peak areas of the separated compounds were integrated automatically. Mass Spectrum Library 2014 for GCMS (O2125401310) was used to identify the separated compounds by comparing the mass spectra obtained with mass spectra of known compounds stored in the library database. The content of each component of the epicuticular waxes was expressed as a percentage of total amounts.

GC-MS analysis of each sample was carried out in triplicate. Analyzed parameters such as a percentage of the different compounds in the epicuticular waxes were processed using variance method (ANOVA) factorial experiment, and the differences between means were tested with Tukey's HSD. All differences were considered to be statistically significant at $P < 0.05$.

## Results

Gas chromatography analysis of chloroform extracts of the fruit epicuticular waxes showed a similar distribution of different hydrocarbons in the waxes of the "Red Heaven" cultivar and both hybrid forms (Fig. 1).

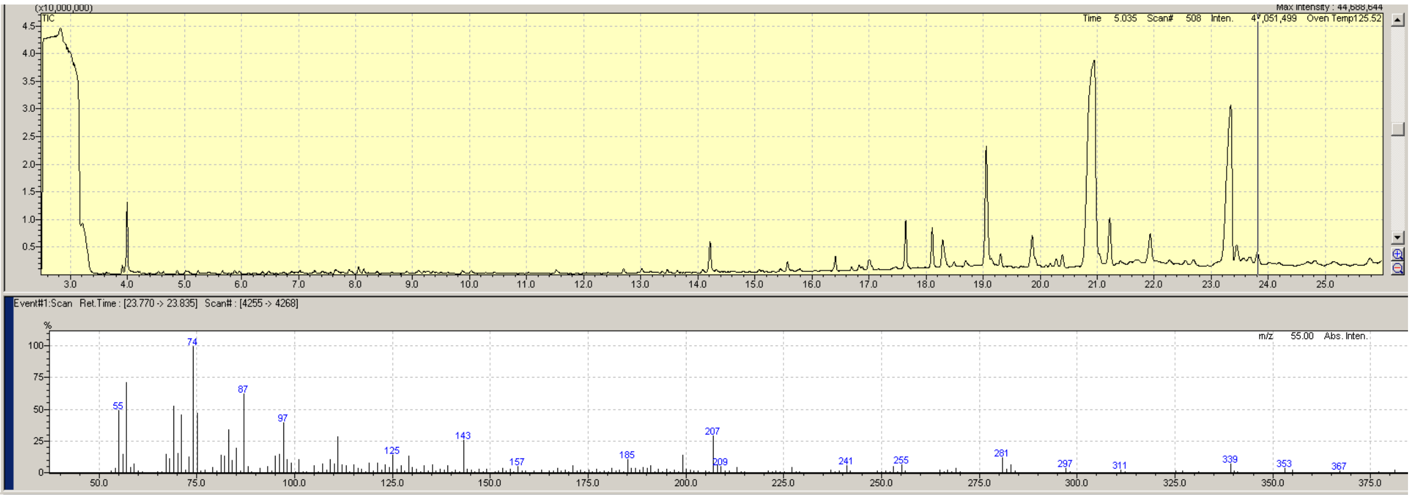


**Fig. 1.** Chromatogram of GC-MS analysis of the epicuticular wax extracts from the surface of peach fruits (typical distribution of the hydrocarbons for all studied samples)

The identification of hydrocarbons and analysis of GC-MS results revealed that the dominant components in the composition of epicuticular waxes of peach fruits were *n*-alkanes with an even and odd number of carbons in the range from C27 to C60. Some alkanes with an even number of carbons were represented by several isomers (Table 1).

**Table 1.** Content of the *n*-alkanes detected in the extracts of fruit epicuticular wax of the genus *Prunus* cultivar and hybrids (% of the total) (Mean ± SE, $n = 3$, $P < 0.05$)

| Compounds | Retention time, min | Plant cultivars and hybrids name | | |
|---|---|---|---|---|
| | | "Red Heaven" cult. | Hybrid I | Hybrid II |
| 2-Methyl-Hexacosane $C_{27}H_{56}$ | 17.631 | – | 7.25 ± 0.22 | – |
| Nonacosane$C_{29}H_{60}$ | 19. 024 | – | 13.29 ± 0.56 | – |
| Triacontane$C_{30}H_{62}$ | 16.874 | 1.38 ± 0.05 | – | – |
| Hexatriacontane $C_{36}H_{74}$ | 19.054 | 10.91 ± 0.59 | – | 16.94 ± 0.74 |
| | 20.790 | 22.18 ± 0.69 | 32.38 ± 0.66 | – |
| Tetracontane $C_{40}H_{82}$ | 16.410 | – | – | 1.97 ± 0.09 |
| | 17.642 | 24.82 ± 1.04 | – | 8.89 ± 0.46 |
| | 19.038 | 26.02 ± 0.78 | – | – |
| Tetrapentacontane $C_{54}H_{110}$ | 20.879 | 4.05 ± 0.21 | – | 42.81 ± 1.89 |
| | 23.246 | 2.07 ± 0.08a | 14.05 ± 0.60b | 14.43 ± 0.74b |
| Hexacontane $C_{60}H_{122}$ | 21.808 | – | – | 2.12 ± 0.08 |

*Note*: the same letters indicate statistically insignificant differences in the compared pair's means according to the Tukey criterion (HSD).

Alkanes with an odd number of carbon atoms (2-methyl-hexacosane and nonacosane) were detected only in the waxes of hybrid I fruits. However, alkanes with an even number predominated in these waxes (69% of all alkanes). Alkanes with a chain length of C36 (hexatriacontane isomers) were found in waxes of all studied fruits, making up the largest part in the wax of fruits of hybrid 1 (48% of all alkanes). Isomers of tetracontane (alkane C40) were present in the fruits of the "Red Heaven" variety and hybrid 2, accounting for 56% and 13% of the total alkanes, respectively absent in the waxes of fruits of hybrid 1. The proportion of tetrapentacontane (alkane C54) isomers was lower in the "Red Heaven" and hybrid I wax (7% and 21% of all alkanes, respectively), while in the wax of the fruits of hybrid II these compounds occupied a dominant position (66% of all alkanes). Alkane C60 (hexacontane) was found only in the epicuticular wax of hybrid II fruits, accounting for 2.4% of the total alkanes.

Minor classes of the compounds detected in fruit epicuticular waxes were the fatty acids, alkenes, aldehydes, and esters, which were observed not in each but specific wax only (Table 2). The remaining unidentified compounds varied from 4% to 7% in fruit epicuticular waxes of different genus Prunus plant*s*.

**Table 2.** Content of less abundant hydrocarbon classes in the extracts of fruit epicuticular wax of the genus *Prunus* cultivar and hybrids (% of the total) (Mean ± SE, $n$ = 3, P < 0.05)

| Compounds | Retention time, min | Plant species and hybrids names | | |
|---|---|---|---|---|
| | | "Red Heaven" cult. | Hybrid I | Hybrid II |
| Fatty acids: | | | | |
| Hexadecanoic acid $C_{16}H_{32}O_2$ | 14.204 | – | – | 1.15 |
| Alkenes: | | | | |
| 17-Pentacontene $C_{35}H_{70}$ | 18.275 | 2.68 ± 0.13 | 8.80 ± 0.33 | – |
| Aldehydes: | | | | |
| Eicosanal$C_{20}H_{40}O$ | 22.528 | – | – | 2.31 ± 0.12 |
| Esters: | | | | |
| Phthalic acid butyl-decyl ester$C_{22}H_{34}O_4$ | 14.321 | – | 4.45 ± 0.14 | – |
| Phthalic acid di-n-octyl ester$C_{24}H_{38}O_4$ | 18.101 | 2.11 ± 0.09a | 14.22 ± 0.65a | 2.52 ± 0.15b |
| Unidentified compounds (% of total) | | 3.78 ± 0.17a | 5.47 ± 0.18b | 6.91 ± 0.25c |

*Note*: the same letters indicate statistically insignificant differences in the compared pair's means according to the Tukey criterion (HSD).

The C16 fatty acid (hexadecanoic acid) and the C20 fatty aldehyde (eicosanale) were present only in the epicuticular wax of hybrid II, while the C35 alkene (17-pentacontene) was detected in the waxes of the "Red Heaven" and hybrid I fruits. Unidentified components were found in all studied peach fruits' waxes, reaching the highest value in the wax of hybrid 2 (7% of the total).

## Discussion

Fruit epicuticular wax composition of *P. persica* "Red Heaven" cultivar and the hybrid forms demonstrated significant differences. Differences in the composition and ratio of hydrocarbon components of fruit waxes of *P. persica* "Red Heaven" cultivar and the hybrids are consistent with the known data (Trivedi et al., 2019) on the variability of these parameters in waxes of fruits of other species. Belge et al. (2014) found significant quantitative differences with certain hydrocarbon compounds in the composition of cuticular waxes from melting and non-melting peach varieties. According to data reported by Wu et al. (2018), the wax composition and concentration varied dramatically among the fruits of 35 pear cultivars belonging to five different species and hybrid interspecies.

The studied peach cultivar and hybrids' epicuticular waxes were almost absolutely dominated by the long-chain *n*-alkanes (C36, C40, and C54), which is consistent with the known data. The dominance of *n*-alkanes, together with other compounds, was found in various plant species' fruit waxes. Belge et al. (2014) characterized alkanes *n*-tricosane and *n*-pentacosane as one of the most prominent fruit cuticular wax components from melting and non-melting peach cultivars. In mandarin fruit epicuticular waxes, fatty acids and alkanes have been identified as the most abundant components (Ding et al., 2020). An explanation of this pattern can be contained in the assumption of Fernández et al. (2016) that the non-polar compounds with low solubilities, such as alkanes, can migrate from the cell wall to the epicuticular wax layer, while the polar compounds (i.e., alcohols, acids, esters) having the hydrogen bonds, will be held in the inner layer of the cuticular waxes.

Many authors regard the high level of alkane accumulation in the epicuticular waxes of fruits as one of the reasons for the high fruit susceptibility to the action of some pathogenic fungi. For example, Silva-Moreno et al. (2016), during the *in vitro* studies, found that the fungi *Botrytis cinerea* can use alkanes as a carbon source, and these aliphatic compounds enhance the growth of the pathogen. The reason for the high susceptibility of ripening peach fruits to the causative agent of moniliosis, following Lino et al. (2020), is the higher level of alkanes in cuticular waxes in the final stage of fruit growth before ripening, which can promote fungal growth. Consequently, the high content of long-chain alkanes found by us in the epicuticular waxes of ripening peach fruits, especially the "Red Heaven" variety and hybrid 2, could be one of the components the fruit's sensitivity to the action of fungal pathogens.

In our work, alkane C29 (nonacosane) was detected in a sufficiently large amount only in the epicuticular wax of the most stable hybrid 1, which makes us assess the possible role of nonacosane in the formation of the fruit cuticle properties, separately from the role of the sum of alkanes. There is convincing evidence of a positive correlation between *n*-alkane C29 in cuticular waxes and cracking tolerance in cherry fruits (Rios et al., 2015). The relationship between peach cracking and the spread of the pathogenic fungus *Monilinia* was shown by Lino et al. (2020), who suggested that resistance factors cease to function in large and early peach fruits cuticle loses its integrity. Considering the hybrid I fruits' ripening begins with the endocarp and the mesocarp's inner layer. Simultaneously, the exocarp remains immature for a long time, and it can be assumed that nonacosan has a positive effect on maintaining the integrity of the fruit cuticle and counteracting pathogenic fungi.

Some authors (Trivedi et al., 2019; Ding et al., 2020) focus on the dependence of the composition and structure of epicuticular fruit waxes on the influence of developmental and environmental factors that affect the protective properties of wax. In our work, the higher molecular weight alkanes hexatriacontane, tetracontane, and tetrapentacontane prevailed in the composition of peach fruit waxes, which could be due not only to the varietal characteristics of peaches but also to the conditions of the environment in which the fruits were formed and ripened. In this regard, attention should be paid to the significant differences between the cuticle of fruits and the cuticle of vegetative organs, emphasized by Martin and Rose (2014), including the often observed absence of stomata and greater thickness than in most leaves. The fruit cuticle's unique properties are confirmed by the significant changes it undergoes during the fruit's storage. For example, Ding et al. (2020) found that such modifications to the cuticle of the mandarin fruit 'Satsuma' affected the structure of all layers of the cuticle; in particular, the accumulation of epicuticular wax increased almost four times during storage for 20 days, and then decreased when storage time increased to 40 days.

Some differences in the component composition of the epicuticular waxes of the fruits of the "Red Heaven" cultivar and the hybrids from other authors' data could also be associated with differences in the stages of maturation of the studied fruits. At least in the mesocarp of peach fruits, Lombardo et al. (2011) identified clear differences in metabolic processes associated with different development stages and postharvest maturation. It has been shown (Li et al., 2014) that differences in the ratio of long-chain components of cuticular waxes can arise as the fruit develops; in particular, alkanes were the main components at the early stage of pear fruit development, while triterpenoids were added to them at a later stage. In peach fruits, as reported by Lino (2016), susceptibility to the pathogen *Monilinia laxa* infection at an early stage of development had a positive relationship with the amount of eicosane (alkane C20) in the cuticular wax, while at the end of fetal development, it was positively associated with tricosan (alkane C23) and a C18:1 fatty acid. In our work, only in the wax of ripening fruits of unstable hybrid 2 was a fatty acid (hexadecanoic acid C16:1) revealed, which can be regarded as a factor in increasing the susceptibility of fruits to fungal diseases.

In the epicuticular waxes composition of all peach fruits we studied, the only aldehyde (eicosanal C20) was found in the wax of hybrid II and, according to the known data, could be associated with the sensitivity of the fruits of this hybrid to fungal pathogens. It has been established (Zabka et al., 2008) that hexacosanal from cuticular wax of barley leaves and octacosanal from the wax of wheat leaves can induce differentiation structures of fungal infection, respectively, *Blumeria graminis* and *Puccinia graminis*. On the contrary, the absence of long-chain aldehydes in the cuticular wax of mutant corn leaves hampered the development of the pathogen *B. graminis* while applying a spray with *n*-hexacosanal (C26-aldehyde) to the leaf surface completely restored fungal germination (Hansjakob et al., 2011). In mature peach fruits, susceptibility to moniliosis was associated with the presence of C22 fatty aldehyde (docosanal) in fruit cuticular wax (Lino, 2016). Earlier, when studying the composition of epicuticular waxes of plant leaves of the genus *Prunus*, we showed (Khromykh et al., 2020) the presence of C18-aldehyde (octadecanal) only in the wax of *P. dulcis* leaves, which was characterized as the most susceptible to clasterosporium disease.

## Conclusion

Component composition of the epicuticular fruit wax of *P. persica* "Red Heaven" cultivar and hybrids that were known for their unequal susceptibility to fungal pathogens showed notable differences. Simultaneously, a common characteristic can be considered the predominance of long-chain alkanes in waxes of all studied ripening fruits.

The cuticular wax of the most stable hybrid 1 contained a significant portion of alkanes with an odd number of carbons (2-methyl-hexacosane C27 and hexacosane C29), which can be regarded as a factor contributing to the preservation of cuticle integrity and, thus, counteracting the development of pathogenic infection. The epicuticular fruit wax of the "Red Heaven" cultivar contains the highest total amount of alkanes, including long-chain alkanes C40 and C54, the accumulation of which may be one of the components of fruit sensitivity to the action of pathogenic fungi. The waxes of ripening fruits of hybrid 2 contained the highest amount of very-long-chain alkanes, including hexacontane (alkane C60), and fatty acid (hexadecanoic acid C16:1), and fatty aldehyde C20 (eicosanal), which together could cause cuticle damage and high susceptibility of fruits to fungal diseases.

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