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Effects of anti-herbivore resistance on sensory characteristics and ripening of strawberry

Johan A. Stenberg[a,*], Paul A. Egan[a], José Mora[b], Sonia Osorio[b], José G. Vallarino[b], Karin Wendin[c,*]

[a] Department of Plant Protection Biology, Swedish University of Agricultural Sciences, Box 190, SE-23422 Lomma, Sweden
[b] Departamento de Biología Molecular y Bioquímica, Campus de Teatinos, Instituto de Hortofruticultura Subtropical y Mediterránea "La Mayora", Universidad de Málaga-Consejo Superior de Investigaciones Científicas, Campus de Teatinos, 29071 Málaga, Spain
[c] Department of Food and Meal Science, Kristianstad University, SE-29188 Kristianstad, Sweden

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ABSTRACT

Plant resistance to agricultural pests is a fundamental element of sustainable crop protection. However, concerns have been raised that strategies to increase resistance may involve phytochemicals that impact fruit ripening and the sensorial perception of the fruit. Here, we experimentally tested for these putative resistance effects by contrasting susceptible varieties of strawberry (*Fragaria vesca*) with varieties that were either constitutively resistant to pest insects or with resistance induced with jasmonic acid (JA). GC-MS analysis identified 11 volatile compounds, including alcohols, aldehydes, lactone, terpenoids, and esters, which showed higher concentrations in fruits from resistant/induced plants. Fruits from induced plants ripened faster in the field. In sensory analyses, using a trained analytical panel, some variation between the sensory profiles of the strawberry varieties was detected, but we found no systematic correlations between sensory attributes and the level of plant resistance/induction in the varieties. These results suggest that increased plant resistance comes with positive effects of early ripening, while not strongly affecting the overall sensory experience.

1. Introduction

Domesticated food crops are typically susceptible to pest organisms, leading to substantial yield losses in the absence of synthetic pesticides (Oerke, 2006). However, as pesticides have become more strictly regulated in recent years, increased attention has been placed on the intrinsic resistance of food crops (Stenberg, 2017; Smith, 2021).

Phytochemical resistance traits can be either constitutive or up-regulated (hereafter 'induced') by external application of various chemicals, such as plant hormones like jasmonic acid (JA) (Zhang et al., 2018; Karban 2020). Apart from elevating the plant's resistance level (Asghari, 2019), such JA induction may also accelerate fruit ripening (Peña-Cortés et al., 2005; Jia et al., 2016), but this desirable synergy still remains unexplored for most crops. Constitutive resistance, on the other hand, is typically optimized during plant breeding for constant expression in the plants. Unfortunately, however, many plant traits that confer resistance against pests have been weakened or removed during the domestication process (Chen et al., 2015; Moreira et al., 2018). The selection against resistance traits may, to some extent, have been a conscious and active strategy by breeders, because such traits have been linked to yield penalties, bitterness, toughness and other negative sensory attributes that are undesirable to human consumers (Chen et al., 2015; Moreira et al., 2018).

Although plant resistance has historically decreased in domesticated crops, the current focus on integrated pest management (IPM) calls for recharging food crops with higher levels of resistance—even to the level of wild plants—to reduce pesticide dependence (Palmgren et al., 2015; Smith, 2021). While such an aim is worthy of earnest consideration, few attempts have been made to test experimentally sensory consequences and fruit ripening in response to elevated resistance. Such considerations are important because consumers may discriminate against cultivars with unsatisfactory attributes. In a previous study, we showed that, when ranking different strawberry attributes, fruit flavor is the single most important one for consumers (Wendin et al., 2019), while, e.g., visual appearance and pesticide-free production were of lower importance. Thus, replacing pesticides with strong plant resistance does not seem viable in a market economy if that transition comes at the cost of flavor.

* Corresponding authors.
E-mail addresses: johan.stenberg@slu.se (J.A. Stenberg), karin.wendin@hkr.se (K. Wendin).

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Phytochemical resistance compounds that are likely to affect food sensory properties include, *inter alia*, phenolics, tannins, terpenoids, esters and lipids (Jouquand et al., 2008; Lopez Pinar et al., 2017). However, as plant resistance comes in many forms (e.g., chemical, mechanical, and phenological traits: Stenberg and Muola, 2017), several types of resistance may involve traits that have low or no negative implications for human consumers. These acceptable traits are likely to include e.g., some chemical metabolites with little or no effect on flavor. Depending on the crop and the aim of crop breeding, such traits may be preferred or avoided when optimizing new cultivars for resistance to herbivores. To make informed decisions in breeding programs, it is important that 'problematic' resistance compounds are identified and replaced with other functional resistance traits. Genome editing for individual plant compounds is sometimes complicated, but not impossible even for polyploid strawberry (Sánchez-Gómez et al., 2022).

Chewing pest insects (including sawflies and leaf beetles) typically cause very high amounts of damage to strawberry plants in northern Europe (Muola et al., 2017). Fortunately, screening a large number of strawberry genotypes, Weber et al. (2020a,b) identified several that showed resistance to these pest insects. High resistance is the ability of the plants to avoid or reduce pest damage even in the presence of pests (Stenberg and Muola, 2017). Later, Koski et al. (2021) showed that high plant resistance did not inflict significant yield penalty. In this study, using the same plant material as Weber et al. (2020a,b) and Koski et al. (2021), we tested for the effects of constitutive and JA induced resistance on both fruit ripening and sensory attributes in wild strawberry (*Fragaria vesca*) varieties. We furthermore identified systematic differences in fruit volatiles between resistant and susceptible varieties in order to inform breeders of potential resistance markers and their relationship to sensory attributes. The aim was to bridge knowledge on plant resistance, chemical markers, sensory attributes, and fruit ripening to provide the holistic knowledge base needed for the sustainable development of strawberry production and consumption in the absence of synthetic pesticides.

2. Materials and methods

2.1. Planting material and handling

Based on previous scorings of resistance (Weber et al., 2020a,b; Koski et al., 2021), we selected three very resistant (12F, 34F, and 35F) and four very susceptible (1A, 4A, 8F, and 10A) *Fragaria vesca* genotypes for the current study (Table 1). In 2017, we established an experimental plantation with these plant genotypes covering a total area of 130 × 40 m (i.e., similar to the general size of commercial strawberry plantations) at the Alnarp campus of the Swedish University of Agricultural Sciences in southern Sweden. The six plant genotypes were planted in a random setup that included 60 plots (full design described in Koski et al., 2021). Within plots, the plants were planted pairwise in soil bags (80 × 30 cm; 80% peat + 20% pumice; pH = 6; 1 kg NPK 11.5.18 per m^3; Emmaljunga Torvmull, Vittsjö, Sweden), i.e., with two plants of the same genotype in each bag. All fruits were harvested at the end of June 2017 and all fruits from the same genotype/treatment in each plot were pooled into one biological replicate. Fresh fruits were immediately used for sensory analyses (see below), and other fruits were placed at −80 °C in a freezer until chemical profiling took place.

Effects on pest damage and total yield were previously reported by Koski et al. (2021) and are, therefore, outside the scope of this paper.

Table 1
Strawberry samples included in this study.

Strawberry sample ID	Strawberry genotype	Strawberry resistance	JA treatment
1A	1A	Susceptible	Not treated
1A J	1A	Susceptible	Treated
1A C	1A	Susceptible	Not treated
04A	04A	Susceptible	Treated
8F	8F	Susceptible	Not treated
10A	10A	Susceptible	Not treated
12F	12F	Resistant	Not treated
34F	34F	Resistant	Not treated
35F	35F	Resistant	Not treated

2.2. Jasmonic acid treatment

For each of the six plant genotypes, three plants received an application of jasmonic acid (JA), and three received a control treatment (water). Selection of the treatment and control plants was made at random so as to avoid any confounding effects due to position in the plantation. To ensure that treatment effects would have time to appear, spraying began approximately eight weeks in advance of berry harvest, and application was conducted in two rounds, with 10 days between them. For the JA treatment, whole plants were sprayed with 20 ml of a 1 mM JA (Sigma-Aldrich) aqueous solution containing 0.1% Tween-20 (Sigma-Aldrich) as a surfactant. This volume corresponded to ~140 μg JA g^{-1} leaf fresh weight, which was sufficient to saturate plants to the point of run-off. Control plants were treated with a 0.1% Tween-20 solution only.

2.3. Chemical profiling

In brief, 500 mg of each biological replicate was mixed with 1 ml of NaCl solution (20% w/v) during continuous stirring until the sample was completely thawed and homogenized. After centrifugation (5000 g, 5 min, room temperature), the supernatant was transferred to headspace vial and 5 μl of internal standard (1 ppm solution in HPLC grade methanol of *N*-pentadecane, D32, 98%) was added.

Volatile metabolites were analyzed with an automated headspace-solid-phase microextraction -Gas Chromatograph coupled to an ion trap Mass Spectrometer (HSPME/GC-MS) as previously reported by Pott et al. (2021). The headspace vial was placed in the GC-MS autosampler at room temperature and pre-incubated for 10 min at 50 °C with agitation 17 g. Then, an SPME device was inserted into the vial and incubated for 30 min at 50 °C with the same agitation. Chromatographic separation was performed with a constant He flow with a column of 60 m × 0.25 mm × 1 μm thickness which was operated at 40 °C for 3 min followed by an 8 °C/min ramp to 250 °C and holding at 250 °C for 5 min. For MS, the transfer line and ion source was set to 260 °C and 230 °C, respectively. The ionization energy was set to 70 eV and the recorded mass range to *m/z* 35–220 at 6 scans per s. The MS fragmentation and retention times of the metabolites was compared with pure commercial standards.

2.4. Sensory analyses

Fresh strawberries were used for the sensory analyses. A trained analytical sensory panel consisting of eight assessors was used in this study. The assessors were selected according to the ISO (International Standard Organization) standard 8586-2:2008 (ISO, 2008). The panel used a slightly modified version of the Flavor Profile Method® (Lawless and Heymann, 2010) for assessment of the strawberry samples listed in Table 1. For training, the sensory panel was given test samples and was then instructed to identify and define sensory attributes according to appearance, odor, taste, flavor and texture. Attributes included in the assessment and their definitions are presented in Table 2. The training also included how to perform the sensory testing and then how to rate intensity of each attribute on a scale ranging from 0 to 100, where 0 = attribute not detected and 100 = the highest intensity possible. During the assessment, the samples were presented and consensus regarding each attribute was reached using the intensity scale. All assessors agreed on the placement of each sample along the intensity axis. Each attribute was assessed for all samples, testing attribute by attribute. To refresh

Table 2
Attributes included in the sensory analysis of strawberry samples and their definitions.

Attribute	Definition
Appearance	
Color intensity	Intensity of berry color, more blue color gives a higher score
Shape	Ranges from round to oblong
Odor	
Artificial	Intensity of strange and weird odors
Mature strawberry	Ranges from immature to mature strawberry
Total odor	Intensity of all odors
Taste/Flavor	
Sweet	Intensity of sweetness
Sour	Intensity of sourness
Bitter	Intensity of bitterness
Mature strawberry	Intensity of sweetness
Artificial	Intensity of strange and weird flavors, unnatural
Texture	
Mouth: Firmness	Ranges from soft to firm
Mouth: Astringent	Rough and dry feeling after swallowing

their senses, the assessors took a break between each testing. They had water and neutral wafers to clean the palate and neutralize the senses.

Each assessor signed up for participation after being informed about the samples and the terms of participation: voluntary participation, freedom to leave the test without giving a reason and the right to decline to answer specific questions.

2.5. Statistics

2.5.1. Associations between fruit volatiles, plant resistance and JA induction

The volatile dataset contained many zero values (*ca.* 52%), so it could not be analyzed using approaches assuming a normal distribution. Indicator compound analysis (or multilevel pattern analysis) was, therefore, selected as it is a technique well-suited to this type of data structure; it was implemented using the R package 'indicspecies' (De Caceres and Legendre, 2009). Indicator compound analysis was used to test whether the profile of fruit volatiles differed according to resistance level (i.e., resistant vs susceptible plants) and JA induction (i.e., jasmonic acid treatment vs. control plants). Compound association values (i.e., point-biserial correlation coefficients) and their corresponding *p*-values (testing the null hypothesis that the correlation is zero) were generated using the 'multipatt' function. These values were generated on the basis of 999 permutations, and using a corrected correlation coefficient (specified as 'r.g' in multipatt). This correlation coefficient is similar to Pearson correlation and is likewise bounded between zero and one.

Individual linear mixed effects models (LMMs) were used to further analyze the subset of compounds that were identified as important in the indicator compound analyses. LMMs were fitted in the lme4 package (Bates et al., 2015) with the factors "resistance level" and "plant genotype" as random effects. Interaction effects between these two factors were only retained in the model if significant alongside one other factor. Models were validated by visual and statistical assessment of the model residuals to ensure these were normally distributed and showed equal variance across the factor levels.

2.5.2. Association between sensory perception and resistance

Principal component analysis (PCA) was undertaken using Panel Check V 1.4.2, Nofima, Norway to obtain an overview of the results. Furthermore, a series of linear regression models was used to test the association between each sensory trait as a dependent variable and with genotype resistance level (i.e., resistant or susceptible) as a predictor variable.

2.5.3. Effect of JA induction on fruit ripening

A two-tailed paired *t*-test was used to determine whether plants receiving jasmonic acid application had significantly more or fewer unripe fruit remaining compared to control plants after an interval of 30 days.

3. Results

3.1. Associations between fruit volatiles, plant resistance and JA induction

In total, 82 volatile compounds were identified from GCMS analysis of the harvested strawberry fruits (Table S1). The chemical diversity was relatively constant across all 55 fruit samples analyzed (overall mean $= 1.64 \pm 0.99$ SD), and did not vary according to plant resistance level ($t = -0.67$, $p = 0.522$), jasmonic acid induction ($t = -1.02$, $p = 0.312$), or their interaction ($t = 0.054$, $p = 0.957$). Genotypic variation in chemical diversity was also not apparent ($\chi^2 = 0.14$, $p = 0.707$).

From this profile of 82 volatile compounds, indicator compound analysis identified an initial sub-set of 14 compounds that were significantly associated with plant resistance level (i.e., either resistant or susceptible genotypes) or jasmonic acid induction (control or induced plants) (Fig. 1, Table 3). Subsequent analysis of these compounds in mixed models (controlling for plant genotype as a random factor) confirmed that 11 compounds varied significantly according to either plant resistance level or jasmonic acid induction (Table 3). No significant interactions were found between these variables during the model-fitting stage (see Methods), and compound levels varied according to plant genotype in seven instances.

3.2. Sensory analyses

The results from the sensory analyses of fresh strawberries are illustrated in Figs. 2 and A1. Fig. 2 shows the sensory profiles of all strawberry genotypes and Figure A1 the PCA scores and loadings. PC 1 explains 55.6%, while PC 2 explains 18.9% of the variation in the data. Interestingly, the susceptible strawberry genotype 1A (incl. 1AC and 1AJ) can be described as being oblong and having quite low color intensity, but was scored high in sweetness and mature flavor and low in sourness and bitterness. Genotypes 34F (resistant) and 8F (susceptible) are characterized by a round shape and a high color intensity. These two genotypes were allocated the lowest scores in sweetness and total odor and the highest in sourness, bitterness and astringency. However, the resistant genotype 35F was allocated the highest astringency, bitterness and sourness scores; it also received low scores for sweetness and total odor. The susceptible genotype 10A received quite low scores for all tastes and flavors, except sweetness, while the resistant genotype 12F received average scores for the sensory attributes. The sensory effects of JA induction can be considered negligible as discerned from the PCA scores and loadings in Fig. A1, where Genotype 1A control (1AC) and JA induced fruit (1AJ) were scored almost identically.

3.3. Effect of jasmonic acid on fruit ripening

The fruit of JA-treated plants ripened significantly quicker (*ca.* 15%) than that of control plants (paired *t*-test: $t = -5.42$, $p = 0.003$), and this pattern was consistent across all six genotypes (Fig. 3). On the day of harvest, JA plants had an average of 19.8 ($\pm$4.1 SE) berries either ripe or remaining on plants, in comparison to an average of 23.2 ($\pm$4.5 SE) on control plants.

4. Discussion

Strong intrinsic plant resistance is key for sustainable production of food crops in general (Smith, 2021) and strawberry in particular (Muola et al., 2017; Weber et al., 2020a,b). The outcome of this study shows that

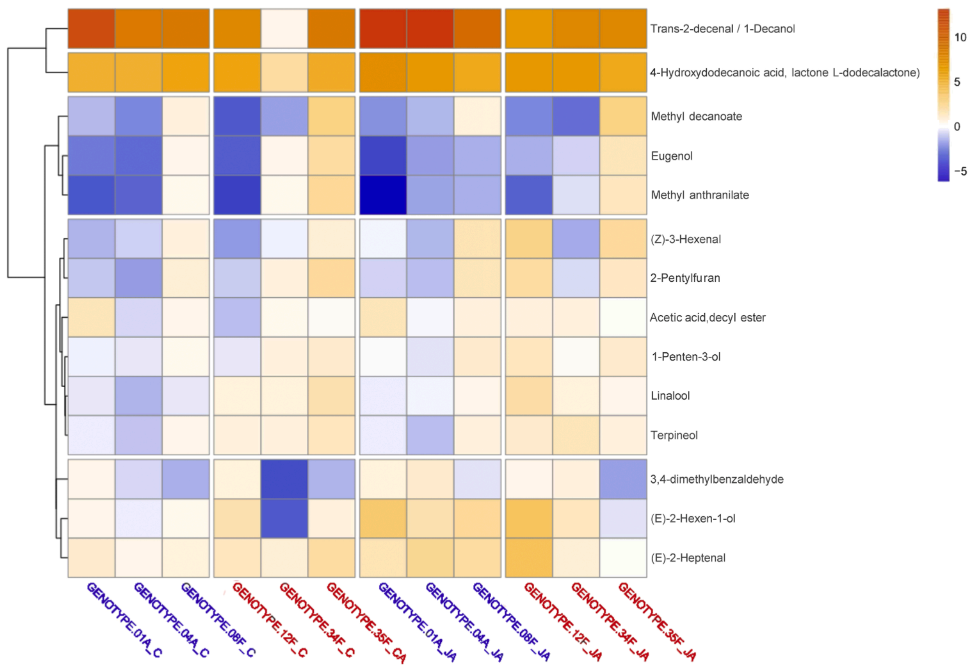

Fig. 1. Heatmap visualization of woodland strawberry (*Fragaria vesca*) metabolites identified in fruit from six genotypes (1A, 4A, 8F, 12F, 34F, 35F), of which resistant genotypes are indicated with red labels, and susceptible ones with blue labels. The six columns to the left show control (C) samples (sprayed with water before harvest), while the six columns to the right show samples sprayed with Jasmonic Acid (JA) before harvest. Only metabolites with significant variation between genotypes and/or treatments are included in the heatmap. Metabolites are grouped by clusters using Pearson correlation coefficients. The colors in the matrix represent the mean values of the metabolite intensities which have been normalized and Log transformed.(For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 3
Association between volatile compounds and 'plant resistance level' (susceptible, resistant) and 'jasmonic acid induction' (control, treatment) in the fruit of wild strawberry (*Fragaria vesca* L.). Association analysis was used to sub-select a reduced number of volatiles from the initial 82 compound set, after which, the 'resistance' and 'induction' factors were assessed in linear mixed models (LMMs) controlling for plant genotype as a random effect. Interactions between the factors were also examined, but were insignificant and were not included in any model. Positive LMM t-values indicate that compound levels were higher in susceptible plants and jasmonic acid-treated plants, and negative values that levels were higher in resistant plants or non-treated control plants.

Compound	Association analysis resistance	Association analysis Induced defense	LMM resistance $-t$ / p-value	LMM induced defense $-t$ / p-value	LMM genotype random effect $-\chi^2$ / p-value
4-Hydroxydodecanoic acid, lactone (γ-dodecalactone)	–	0.36 / 0.006 **	0.38 / 0.755	3.14 / 0.003 **	5.17 / 0.023 *
2-Hexen-1-ol, (E)-	–	0.34 / 0.008 **	0.07 / 0.948	2.99 / 0.004 **	6.46 / 0.011 *
1-Penten-3-ol	–	0.28 / 0.018 *	−1.02 / 0.375	2.39 / 0.021 *	2.08 / 0.149
Trans-2-decenal / 1-Decanol	–	0.28 / 0.046 *	2.01 / 0.137	2.42 / 0.019 *	1.02 / 0.312
(Z)-3-Hexenal	–	0.27 / 0.023 *	−1.23 / 0.291	2.19 / 0.034 *	2.65 / 0.104
(E)-2-Heptenal	–	0.26 / 0.039 *	−0.65 / 0.551	2.29 / 0.027 *	9.72 / 0.002 **
3,4-dimethylbenzaldehyde	–	0.27 / 0.047 *	0.71 / 0.529	2.160 / 0.036 *	0.860 / 0.354
Terpineol	0.43 / 0.004 **	–	−3.45 / 0.001 **	0.58 / 0.562	0 / 1†
Methyl anthranilate	0.43 / <0.001 ***	–	−1.12 / 0.326	−2.25 / 0.029 *	30.60 / <0.001 ***
Linalool	0.38 / <0.001 ***	–	−2.75 / 0.008 **	0.22 / 0.830	0 / 1†
Eugenol	0.36 / 0.008 **	–	−1.04 / 0.357	−0.60 / 0.552	17.21 / <0.001 ***
Acetic acid, nonyl ester	0.28 / 0.044 *	–	−2.15 / 0.036 *	−1.66 / 0.104	0 / 1†
2-Pentylfuran	0.28 / 0.046 *	–	−1.00 / 0.370	−0.79 / 0.434	8.42 / 0.004 **
Methyl decanoate	0.273 / 0.041 *	–	−0.76 / 0.489	0.21 / 0.836	19.40 / <0.001 ***

† Random effects not estimated due to singularity of fit.

elevated resistance is likely to have positive side effects, in addition to sustainable pest control.

First, strawberry fruits developing on JA-induced plants ripened more rapidly than fruits on control plants. Such effects of JA have previously been found for grapes (Jia et al., 2016) and garden strawberry (Yilmal et al., 2003), for example, but have, until now, never been tested for woodland strawberry. Fast ripening reduces the time until harvest and should thereby limit plants' exposure time to pests and pathogens, leading to higher cropping security. Moreover, in Scandinavia, the market demand for fresh strawberries is high early in the season, leading to peak prices around midsummer (i.e., ~ June 20) whereafter the prices drop dramatically. In fact, the national Swedish production is mainly driven by consumer demand around a couple of days in connection with the holiday of midsummer (Bengtsson, 2021). Strawberry growers, thus, run a race against time to be able to harvest the fruit before midsummer. The JA-induced rapid ripening may, therefore, enable growers to harvest fruit a few days earlier and allow them to sell their yield in time for peak demand. Such a development could be economically very important for Scandinavian growers competing with more Southern growers who can start their growing season earlier in the spring.

Second, when comparing the bouquets of fruit volatiles released by resistant vs. susceptible strawberry varieties, we found systematic differences in the concentrations of 11 volatile compounds (Table 3). Three of these compounds were found to have higher concentrations in constitutively resistant over susceptible varieties. Although the relationships between individual compounds and scores from the trained sensory panel could not be evaluated, we note that one of these compounds (acetic acid) is likely to contribute to the attribute "sour" and weak acids normally contribute to an intense sourness (Da Conceicao Neta et al., 2007), while two other compounds (terpineol and linalool) are likely to contribute to the "artificial" attribute, with odors associated with terpenes in flowers (Furia and Bellanca, 2019). The latter two

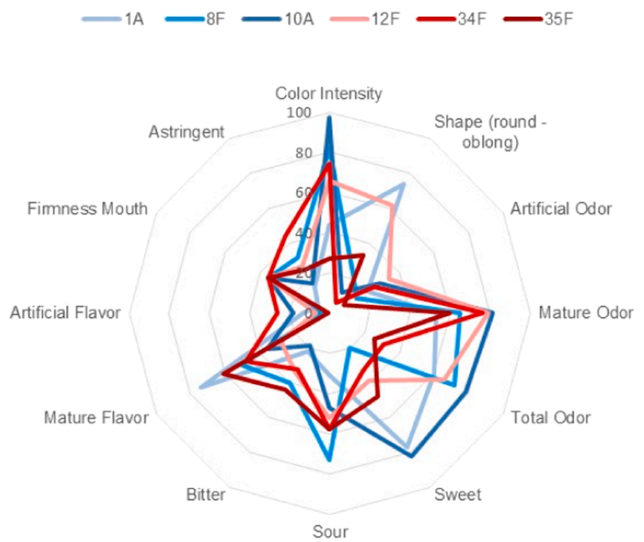

Fig. 2. Sensory profiles of the six strawberry genotypes. The three susceptible genotypes (1A, 8F, 10A) are indicated with blue lines, while the three resistant genotypes (12F, 34F, 35 F) have red lines.(For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

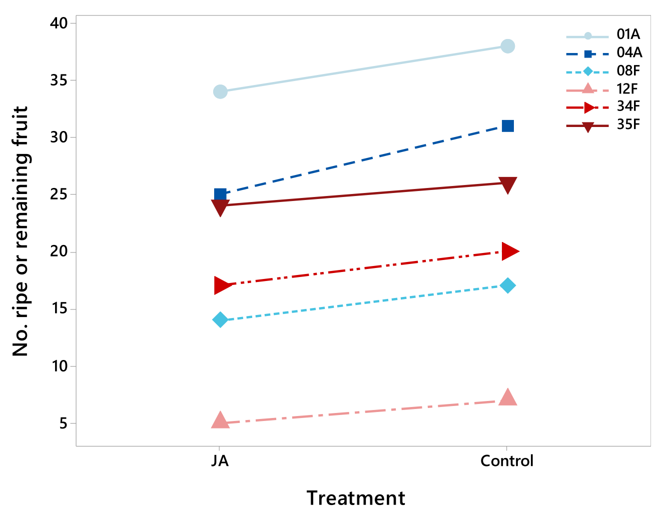

Fig. 3. Effect of jasmonic acid (JA) treatment on the speed of fruit ripening in wild strawberry (*Fragaria vesca*). Plotted is the outcome of a paired *t*-test (total number of berries per Genotype) showing that JA increased the speed of ripening for each genotype, as indicated by the significantly fewer number of berries that remained on plants at the time of harvest (which was made once at the end of the 8-week treatment period).

compounds are likely to contribute to "total odor".

Eight compounds were significantly induced by jasmonic acid. The sensory roles of some of these compounds are unclear, but three of them, i.e., 4-hydroxydodecanoic acid, (E)-2-heptenal and 3,4-dimethylbenzaldehyde, are likely to contribute to the "mature strawberry" and "total odor" attributes (Furia and Bellanca, 2019). The first two of these are also likely to contribute to "fruitiness", while the last one probably contributes to "sweet"-like flavor (Furia and Bellanca, 2019). One compound was found in lower amounts following the jasmonic acid application, namely methyl anthranilate. This metabolite has previously been identified as a key compound in causing aroma type differences between garden strawberry (*Fragaria* × *ananassa*) and wild strawberry (*F. vesca*) (Ulrich and Olbricht, 2013), and is likely to contribute to several attributes, including "mature woodland strawberry", "total odor", "sweet", and "fruitiness" (Fraternale et al., 2011). The low amounts of methyl anthranilate in JA-treated plants is especially interesting, because this compound is known to mediate plant resistance to the important strawberry pest *Drosophila suzukii* (Bräcker et al., 2020).

However, while plant resistance may elevate or reduce several individual compounds with known sensory effects, it is not surprising that the individual effects can balance each other out such that the overall sensory effect of resistance becomes blurred and undetectable. The lack of overall sensory effects of resistance is actually good news for breeders and growers aiming to increase plant resistance to reduce pest damage. Our results show that increased resistance at least does not come at the cost of, e.g., reduced sweetness or increased sourness and bitterness as detected by human consumers. In particular, sweetness has been found to be a key factor for sensory experience and approval (Fan et al., 2021), while many consumers are averse to intense bitterness (Drewnowski and Gomez-Carneros, 2000). While resistance compounds may add value to the sensory profiles of certain crops, such as grape, we do not assume that such effects would be well received for strawberry (Fan et al., 2021; Bhat et al., 2015). For most soft fruit crops, such negative effects would probably preclude their application as part of a strategy to combat pests sustainably.

5. Conclusions

To conclude, the results of this study show that increased plant resistance has synergetic effects on fruit ripening, while not significantly affecting the flavor of strawberry. In addition, a recent study (Koski et al., 2021) showed that these focal resistance traits effectively reduce pest damage and do not inflict yield penalties on strawberry. Taken together, these are important findings underlining the fact that increased plant resistance can be utilized as a basis for sustainable production of strawberries of high food quality.

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CRediT authorship contribution statement

Johan A. Stenberg: Conceptualization, Writing – original draft, Funding acquisition, Investigation, Methodology, Validation, Writing – review & editing. **Paul A. Egan:** Conceptualization, Data curation, Formal analysis, Writing – original draft, Funding acquisition, Investigation, Methodology, Validation, Writing – review & editing. **José Mora:** Funding acquisition, Investigation, Methodology, Validation, Writing – review & editing. **Sonia Osorio:** Conceptualization, Funding acquisition, Investigation, Methodology, Validation, Writing – review & editing. **José G. Vallarino:** Funding acquisition, Investigation, Methodology, Validation, Writing – review & editing. **Karin Wendin:** Conceptualization, Data curation, Formal analysis, Writing – original draft, Funding acquisition, Investigation, Methodology, Validation, Writing – review & editing.

Declaration of Competing Interest

Authors declare that they have no conflict of interest.

Data availability

We have added the data to a supplementary file included in this submission.

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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.2023.112434.

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