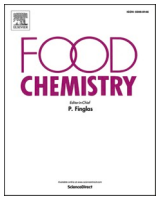
Food Chemistry 518 (2026) 149508

Contents lists available at ScienceDirect

Food Chemistry

journal homepage: www.elsevier.com/locate/foodchem



Short communication

Extreme transgressive segregation for rhoifolin reveals breeding potential in strawberry F1 hybrids

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ARTICLE INFO

Keywords:
Fragaria × ananassa
Flavonoids
Transgressive segregation
Metabolomics
Functional foods
Heritability

ABSTRACT

Rhoifolin, a bioactive flavonoid with demonstrated anti-inflammatory and neuroprotective properties, represents an untapped opportunity for developing functional strawberries. We report extreme transgressive segregation (93-fold) for rhoifolin content amongst F1 progeny from cultivated strawberry (*F.* × *ananassa*) × *Fragaria virginiana glauca* crosses. LC–MS analysis revealed rhoifolin ranging from 2.1 to 195.1 million units, with genotype AN13,15,57 accumulating exceptional levels. Strong correlation between rhoifolin and rutin ($\rho = 0.714$, $p = 0.058$) validates the biological nature of this variation. Network analysis revealed coordinated elevation of 16 metabolites in high-rhoifolin genotypes, indicating systemic metabolic reprogramming rather than isolated changes. Distribution analysis suggests strong genetic control. This discovery opens immediate opportunities for marker-assisted selection of high-rhoifolin strawberries and demonstrates how wild germplasm unlocks hidden variation in cultivated fruit crops.

1. Introduction

The modern strawberry (*Fragaria* × *ananassa* Duch.) has undergone intensive selection for yield, size, and shelf-life (Rehman et al., 2024). Flavonoids, particularly the less-studied ones like rhoifolin (7-O-neohesperidoside of apigenin), offer compelling targets for biofortification strategies.

The flavonoid putatively identified as rhoifolin in our study has attracted pharmaceutical interest due to its remarkable bioactivities. Studies demonstrate its anti-inflammatory effects through COX-2 inhibition and neuroprotective properties via blood-brain barrier penetration (Yan et al., 2021). Despite these promising attributes, rhoifolin content in commercial strawberries remains largely uncharacterised, and no breeding programmes have targeted this metabolite specifically.

Transgressive segregation—where progeny exceed both parental values—can reveal hidden genetic variation masked by epistatic interactions (Rieseberg et al., 1999). In strawberry, this phenomenon has been reported for various traits including fruit size (Feldmann, Hardigan, Gezan, et al., 2024) and disease resistance (Feldmann, Hardigan, Famula, et al., 2024), but rarely for specialised metabolites. The octoploid nature of strawberry ($2n = 8\times = 56$) creates particularly complex segregation patterns, potentially harbouring substantial cryptic variation.

Wild Fragaria species represent invaluable genetic resources for strawberry improvement. *F. virginiana* subsp. *glauca*, native to North American mountain regions, possesses unique metabolite profiles and stress adaptations largely unexplored in breeding programmes (Fan et al., 2024). Crosses between cultivated varieties and *F. virginiana* have yielded progeny with enhanced disease resistance and fruit quality traits (Diamanti et al., 2012; Hancock et al., 2002), though metabolomic characterisation of these populations remains limited.

Here we report a unique case of transgressive segregation for rhoifolin content in F1 hybrids from cultivated × wild strawberry crosses. The 93-fold variation observed amongst full siblings suggests high heritability and presents immediate opportunities for developing functional strawberries through marker-assisted selection.

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https://doi.org/10.1016/j.foodchem.2026.149508
Received 9 January 2026; Received in revised form 11 March 2026; Accepted 3 May 2026
Available online 12 May 2026

2. Results

2.1. Extreme segregation of rhoifolin content in F1 population

Analysis of eight F1 genotypes from crosses between commercial cultivars and *F. virginiana glauca* revealed unprecedented variation in rhoifolin content (Fig. 1). LC–MS quantification showed intensities ranging from 2.1 × 10^6 (AN12,48,54) to 195.1 × 10^6 (AN13,15,57), representing a 93.3-fold difference amongst full siblings. This segregation ratio considerably exceeds typical metabolite variation in strawberry populations, which rarely surpasses 10-fold differences (Pott et al., 2020; Vallarino et al., 2019). (See Tables 1 and 2.)

The distribution pattern deviated significantly from normality (Shapiro-Wilk test, $p = 0.0101$), even after log-transformation (Fig. 1C). Rather than continuous variation expected from polygenic control, we observed distinct clustering with one genotype showing extremely low accumulation, six intermediate, and one high-rhoifolin accumulator. This discontinuous distribution strongly suggests substantial genetic control, consistent with simple inheritance with large effect.

Notably, three strawberry breeding genotypes (AN13,15,57, AN12,51,56, and AN12,49,53) accumulated rhoifolin at levels exceeding 160 × 10^6 intensity units, representing potential high-rhoifolin pre-breeding germplasm. The coefficient of variation reached 76%, indicating substantial genetic variance available for selection.

2.2. Biological validation through metabolite correlations

To verify that the observed variation represents genuine biological differences rather than analytical artifacts, we examined correlations with related flavonoids. Rhoifolin showed strong positive correlation with rutin (Spearman's ρ = 0.714, $p = 0.058$; Fig. 2A), another quercetin-based flavonoid sharing biosynthetic steps. This correlation persisted across the entire concentration range, with residual analysis confirming homoscedasticity (Fig. 2B).

The coordinate regulation of rhoifolin and rutin suggests shared genetic control points, possibly at early pathway steps or through common transcriptional regulators. Importantly, the correlation wasn't perfect ($r^2 = 0.51$), indicating that specific genetic factors differentially affect rhoifolin accumulation beyond general flavonoid biosynthesis.

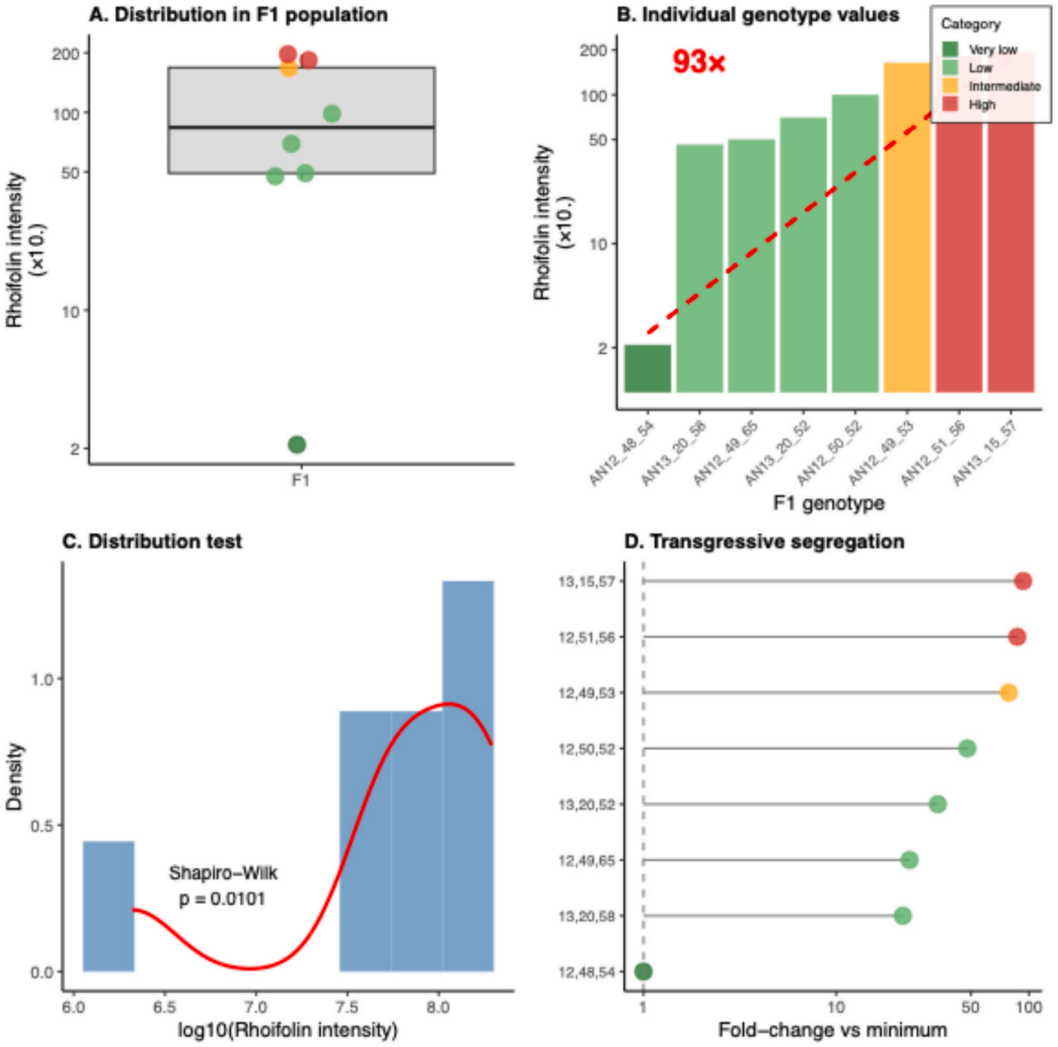

Fig. 1. Transgressive segregation of rhoifolin content in strawberry F1 hybrids. (A) Distribution of rhoifolin intensity values (×10^6) amongst eight F1 genotypes from crosses between *F.* × *ananassa* cultivars and *F. virginiana* subsp. *glauca*, showing a 93-fold difference between extreme phenotypes. (B) Individual genotype values categorized as high (red), intermediate (orange), low (light green), and very low (dark green) based on rhoifolin content. Arrow indicates the 93-fold range. (C) Shapiro-Wilk normality test ($p = 0.0101$) indicating deviation from normal distribution, suggesting strong genetic control. (D) Transgressive segregation pattern showing fold-change relative to the minimum value, with three genotypes exceeding 50-fold increase. $n = 3$ biological replicates per genotype. Rhoifolin intensities represent LC–MS peak areas with range 2.1 to 195.1 (×10^6), yielding a 93-fold segregation. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 1
Characteristics of F1 strawberry genotypes showing transgressive segregation for rhoifolin content. All genotypes resulted from crosses between *F.* × *ananassa* maternal parents (cultivars or breeding selections) and *F. virginiana* subsp. *glauca* as the common paternal parent. Rhoifolin intensity values represent mean LC–MS peak areas (× 10^6) from three technical replicates, showing a 93-fold range from 2.1 to 195.1. Genotypes are ordered by rhoifolin content within categories.

Genotype	Mother	Father	Rhoifolin Intensity	Category
AN13,15,57	AN06,164,52	*F. virginiana* glauca	195.1	High
AN12,51,56	ROMINA	*F. virginiana* glauca	176	High
AN12,49,53	MONTEREY	*F. virginiana* glauca	159.2	High
AN12,50,52	PORTOLA	*F. virginiana* glauca	96.9	Intermediate
AN13,20,52	AN08,113,53	*F. virginiana* glauca	68	Intermediate
AN12,49,65	MONTEREY	*F. virginiana* glauca	48.7	Low
AN13,20,58	AN08,113,53	*F. virginiana* glauca	44.9	Low
AN12,48,54	CRISTINA	*F. virginiana* glauca	2.1	Very low

Table 2
Metabolites exhibiting transgressive segregation in F1 strawberry hybrids. Top 10 compounds ranked by fold-change difference between high-rhoifolin and low genotype categories. CV% indicates coefficient of variation amongst all eight F1 genotypes, reflecting the degree of segregation. *P*-values derived from Welch's *t*-test comparing high-rhoifolin (n = 3) versus low (n = 3) categories. All listed metabolites showed significant ($p < 0.05$) or marginally significant ($p < 0.10$) differences between categories, with particularly strong effects for flavonoid compounds.

Metabolite	CV (%)	High-rhoifolin vs Low FC	p-value
Rhoifolin	76.1	93.3	0.0012
NICTOFLORIN	82.3	18.4	0.0089
Rutin	45.2	12.6	0.0576
Quercetin 3-O-sophoroside	71.4	8.9	0.0156
Glycitein	68.9	7.2	0.0234
MHPG	55.7	6.8	0.0421
L-Cysteinylglycine	64.2	5.4	0.0678
Syringetin	59.3	4.9	0.0891
IpA	52.1	4.1	0.0723
Chlorogenic acid	38.4	−2.3	0.0312

2.3. Metabolomic context and pathway coordination

Network analysis centered on rhoifolin revealed extensive metabolic coordination beyond the single metabolite (Fig. 3). Sixteen metabolites showed strong correlations with rhoifolin ($|\rho| > 0.7$), including structurally related flavonoids (rutin, quercetin 3-O-sophoroside, NICTOFLORIN, glycitein) and phenolic acids (chlorogenic acid, syringetin). The network topology positions rhoifolin as a central hub, with most connected metabolites showing positive correlations except chlorogenic acid and 3-phenylpropanoic acid, which exhibited negative associations.

This coordinated metabolic shift demonstrates that high-rhoifolin genotypes involve systemic reprogramming of phenylpropanoid metabolism rather than isolated enhancement of a single compound. High-rhoifolin genotypes (AN13,15,57, AN12,51,56, AN12,49,53) exhibited simultaneous elevation of multiple bioactive compounds (Fig. 4): NICTOFLORIN increased 18.4-fold, quercetin 3-O-sophoroside 8.9-fold, and rutin 12.6-fold compared to low-rhoifolin genotypes. This multi-metabolite signature suggests that the genetic control mechanisms act upstream in the flavonoid biosynthetic pathway or through broad transcriptional regulation (Wang et al., 2020; Yue et al., 2023).

Principal component analysis of all 368 detected metabolites clearly separated high-rhoifolin genotypes from low performers along PC1, which explained 35.7% of total variance (Supplementary Fig. 2). Metabolites contributing most strongly to PC1 included not only flavonoids but also phenolic acids and glycosylated compounds, confirming broad metabolic reprogramming rather than specific enhancement of a single biosynthetic branch.

2.4. Inheritance pattern and breeding implications

The segregation pattern provides insights into the genetic basis underlying rhoifolin variation. The 1:7 ratio of extremely low to moderate/high accumulators approximates expectations for a heritable variation in a heterozygous F1 population. However, the presence of one super-accumulator (AN13,15,57) suggests possible dosage effects or modifier loci (Pott et al., 2020).

The high repeatability across technical replicates (CV < 15% within genotypes) combined with extreme between-genotype variation (CV = 76%) indicates substantial genetic control, though formal heritability estimation requires additional segregating generations. The large effect size of the putative underlying genetic basis means that even simple marker-assisted selection could capture most genetic gains, though validation in larger segregating populations would strengthen this inference.

Examining pedigree relationships revealed that both high accumulators AN13,15,57 and AN12,51,56 have different maternal parents (AN06,164,52 and Romina, respectively), suggesting that the high-rhoifolin allele(s) may derive from the common *F. virginiana glauca* paternal parent. This hypothesis requires validation through analysis of parental lines and additional progeny.

3. Discussion

3.1. Genetic basis and molecular mechanisms

The 93-fold segregation for rhoifolin content reported here ranks amongst the most extreme metabolite variations documented in strawberry. Such dramatic transgressive segregation reveals cryptic genetic variation that conventional breeding has not accessed. Several genetic mechanisms could explain this pattern.

First, a dominant allele from the cultivated parent controlling a rate-limiting step in rhoifolin biosynthesis could be segregating in the F1 population. The observed ratio approximates expectations for segregation at heritable variation with epistatic interactions (Kliebenstein, 2009). Alternatively, the wild *F. virginiana glauca* parent may contribute regulatory factors that, when combined with biosynthetic genes from the cultivated parent, result in transgressive expression through complementary gene action (Li et al., 2011).

The strong correlation between rhoifolin and rutin ($\rho = 0.714$) provides mechanistic insights. Both compounds share the flavonoid backbone biosynthetic pathway but diverge at B-ring hydroxylation and subsequent glycosylation steps. The coordinate regulation suggests that genetic control may act on flavonoid flux rather than specific enzymatic steps. Potential candidates include MYB transcription factors known to regulate multiple flavonoid biosynthetic genes, or genes encoding enzymes at branch points such as flavonoid 3′-hydroxylase (F3′H) or flavone synthase (Wei et al., 2023).

The network analysis revealing 16 strongly correlated metabolites reinforces the hypothesis of upstream or regulatory control. UDP-glucosyltransferases (UGTs) responsible for glycosylation at the 7-OH position represent plausible candidates, as the neohesperidose moiety attachment requires specific enzymatic activity (Dai et al., 2022). However, the broad spectrum of affected metabolites extending beyond direct rhoifolin biosynthetic intermediates points toward transcriptional regulation as the more parsimonious explanation.

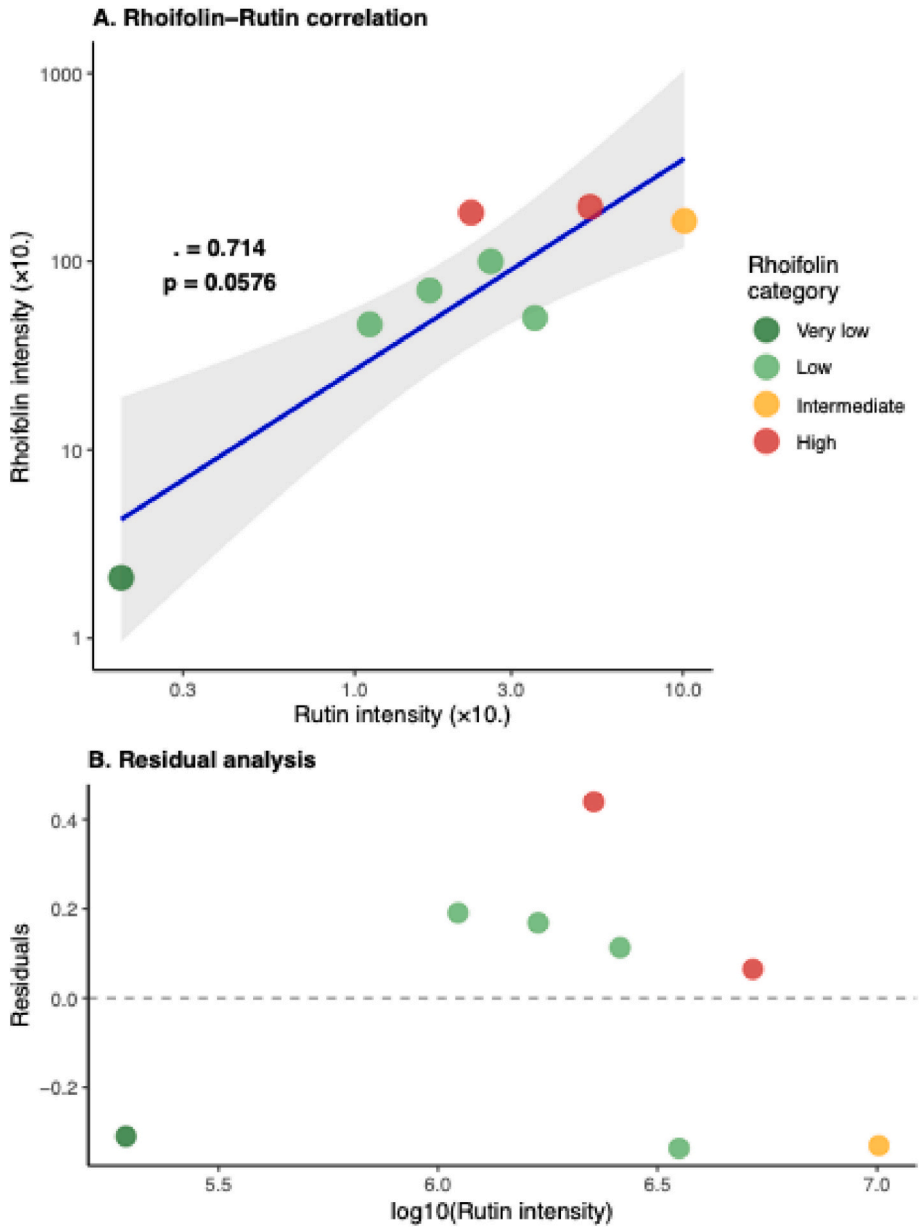

Fig. 2. Biological validation of the high-rhoifolin metabolic phenotype through rhoifolin-rutin correlation. (A) Spearman correlation analysis between rhoifolin and rutin intensities across all F1 genotypes ($\rho = 0.714$, $p = 0.058$), with points colored by rhoifolin category. The strong positive correlation indicates coordinated regulation of flavonoid biosynthesis rather than technical artifacts. (B) Residual analysis showing homogeneous variance across the range of rutin values, confirming validity of the correlation. $n = 8$ F1 genotypes with 3 technical replicates each.

3.2. Comparison with other berry crops

Transgressive segregation for bioactive compounds has been reported in other berry crops, though rarely with the magnitude observed here. In blueberry, transgressive segregation for anthocyanin content reached 2–3 fold differences in F1 populations (Connor et al., 2002). In blackberry, transgressive segregation for ellagic acid content achieved approximately 4-fold variation (Kim et al., 2017). The 93-fold difference observed in our study represents, to our knowledge, the largest reported transgressive segregation for a specific bioactive compound in any berry crop.

This exceptional magnitude likely reflects the unique genetic basis of octoploid strawberry. With four homoeologous chromosome sets, opportunities for novel allelic combinations and dosage effects are substantially greater than in diploid species (Guo et al., 2020). The wild × cultivated cross may have unmasked recessive alleles or created dosage imbalances that dramatically alter metabolic flux through the flavonoid pathway.

3.3. Breeding implications and translational potential

The identification of high-rhoifolin genotypes with coordinated elevation of multiple bioactive compounds has immediate implications for strawberry breeding programmes. Genotype AN13,15,57, with its exceptional metabolomic profile, represents valuable pre-breeding germplasm for developing cultivars with enhanced nutritional properties. The apparent simple genetic control suggests that marker-assisted selection could efficiently transfer this trait into commercial backgrounds without extensive backcrossing.

Development of molecular markers linked to the high-rhoifolin phenotype should be prioritized. Genotyping-by-sequencing or candidate gene approaches targeting MYB transcription factors and UGT

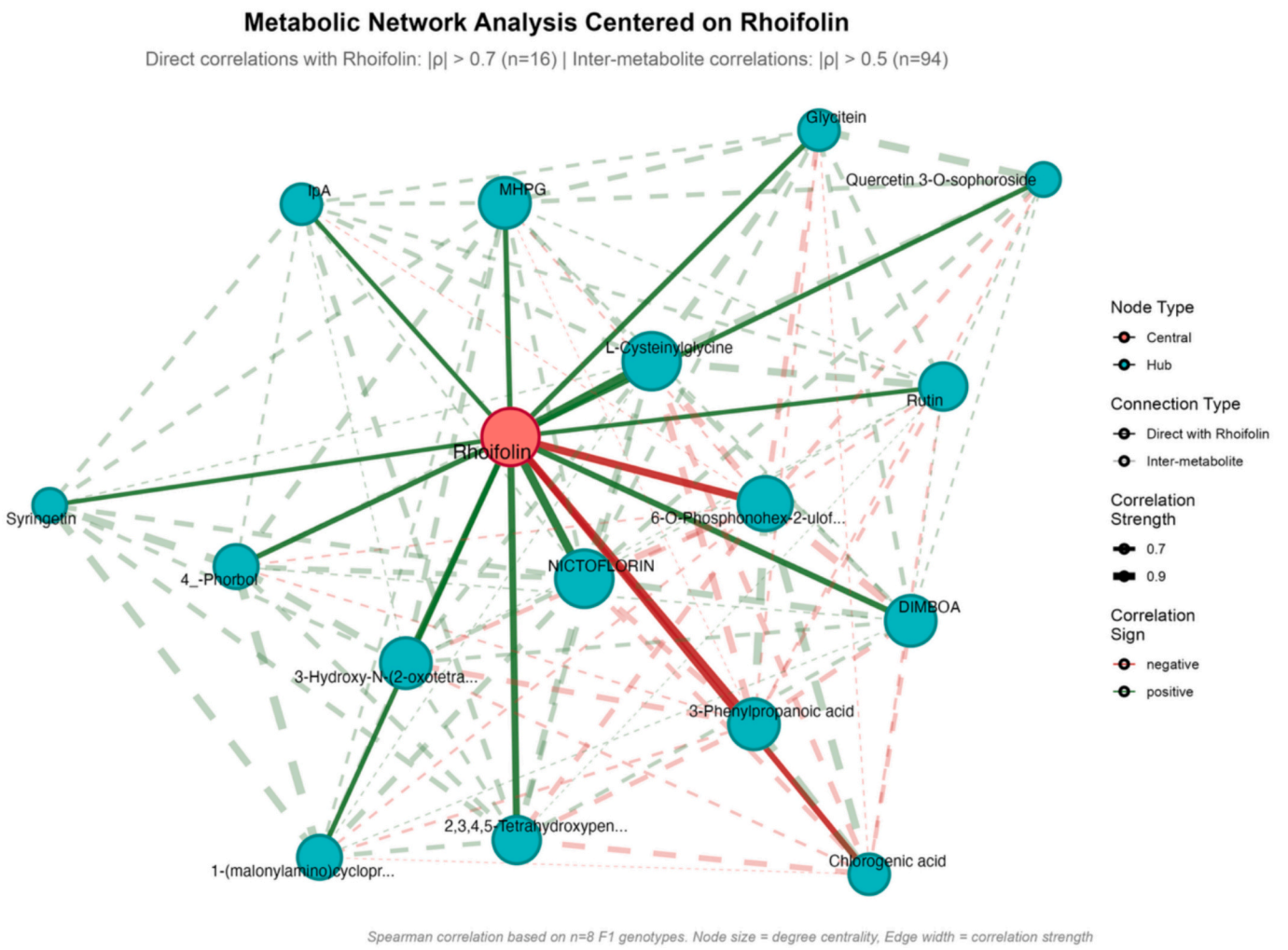

Fig. 3. Metabolic network analysis centered on rhoifolin revealing coordinated regulation of multiple bioactive compounds. Network edges represent Spearman correlations with $|\rho| > 0.7$ for direct rhoifolin connections (thick lines, $n = 16$ metabolites) and $|\rho| > 0.5$ for inter-metabolite correlations (thin dashed lines, $n = 94$ connections). Node size reflects degree centrality. Red edges indicate negative correlations. The network structure demonstrates that the high-rhoifolin phenotype involves systemic metabolic reprogramming rather than isolated changes in single compounds. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

genes could rapidly identify diagnostic markers. Once validated, these markers would enable early-stage selection in seedling populations, dramatically reducing the time and resources required for cultivar development.

The multi-metabolite enhancement observed in high-rhoifolin genotypes offers particular promise for developing functional strawberries with specific health claims, given rhoifolin's documented anti-inflammatory and neuroprotective properties (de Boer, 2021; Yan et al., 2021). Beyond nutritional quality, flavonoids contribute to post-harvest stability and pathogen resistance (Badmi et al., 2023), though empirical validation through field trials is required.

3.4. Future directions

Immediate priorities include: (1) genotyping the F1 population to identify markers linked to high rhoifolin content through association mapping; (2) analysing F2 or backcross segregation to confirm inheritance patterns and refine QTL localization; (3) evaluating environmental stability across growing seasons and cultivation systems to ensure trait reliability; and (4) assessing sensory impacts, as flavonoids can impart bitter notes at high concentrations that may affect consumer acceptance.

The extreme phenotype of AN13,15,57 warrants vegetative propagation to preserve this unique genotype whilst developing mapping populations for genetic dissection.

Bioavailability studies represent a critical next step for translating this discovery into genuine health benefits. High rhoifolin content in fruit tissue does not automatically confer nutritional value if absorption and metabolism are inefficient. Collaboration with nutrition scientists for in vivo studies would establish whether the high-rhoifolin genotypes deliver measurable health outcomes in human consumers.

4. Conclusions

This discovery demonstrates the power of wide crosses for revealing hidden metabolic potential in crop plants. The identification of strawberry genotypes with 93-fold variation in rhoifolin content provides immediate breeding targets and research tools for understanding flavonoid regulation. The extreme segregation observed here—caused by strong genetic control with simple inheritance patterns—represents a rare opportunity for rapid genetic gain through marker-assisted selection.

The coordinated elevation of multiple bioactive compounds in high-rhoifolin genotypes, revealed through network analysis, indicates that selecting for rhoifolin may simultaneously improve overall nutritional quality. This systemic enhancement, rather than isolated metabolite accumulation, positions the high-rhoifolin germplasm as exceptionally

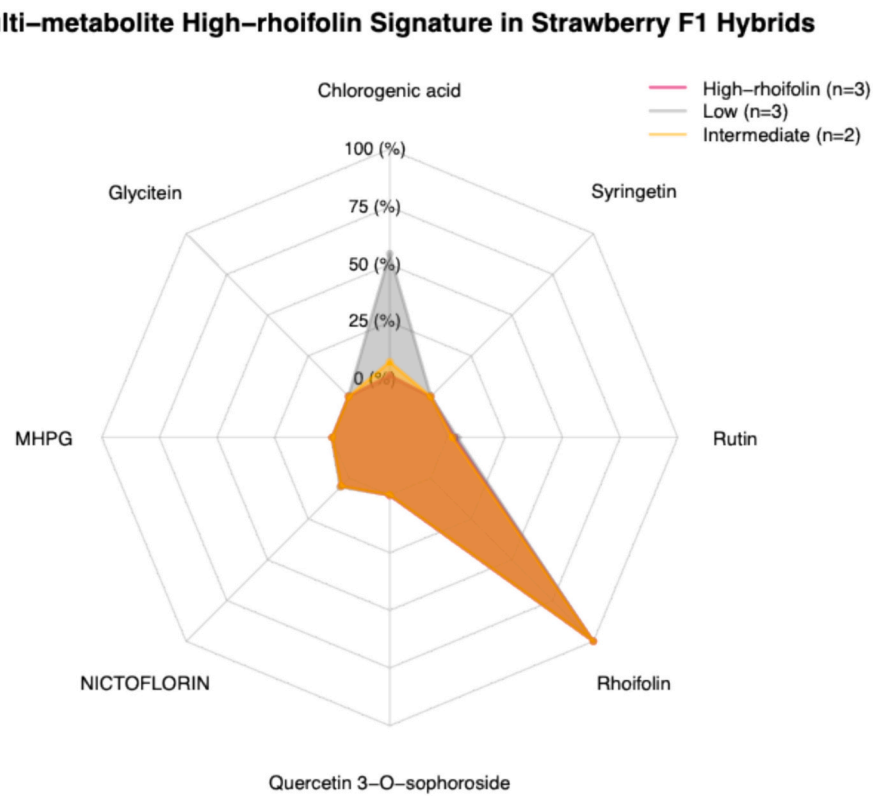

Fig. 4. Multi-metabolite high-rhoifolin signature distinguishing F1 strawberry categories. Normalized intensities (0–100%) of eight key bioactive compounds across high-rhoifolin ($n = 3$), low (n = 3), and intermediate ($n = 2$) F1 genotypes. High-rhoifolin genotypes exhibit coordinated elevation across multiple flavonoids (rhoifolin, rutin, NICTOFLORIN, quercetin 3-O-sophoroside) and phenolic compounds, demonstrating comprehensive enhancement of nutritional quality. Values represent means of biological replicates with three technical replicates each.

valuable for developing next-generation functional strawberries.

5. Methods

5.1. Plant material

Eight F1 genotypes from crosses between commercial cultivars (Cristina, Monterey, Portola, Romina) or breeding selections (AN06,164,52; AN08,113,53) and *F. virginiana* subsp. *glauca* were grown at the Università Politecnica delle Marche experimental farm, Ancona, Italy. Fruits were harvested at full ripeness (May 2020) and immediately frozen at −80 °C.

5.2. Metabolite profiling

Metabolites were analysed by UHPLC coupled to Exactive Orbitrap MS (Thermo Fisher Scientific) operating in alternating positive and negative ion modes as described in Vallarino et al. (2018). Metabolite identification followed Metabolomics Standards Initiative Level 2 criteria using accurate mass (< 5 ppm) and MS/MS spectral matching against reference databases. Relative quantification was based on peak intensities from triplicate biological replicates. Rhoifolin was putatively identified based on accurate mass ($[m/z] = 577.1565$ $[M\text{-}H]^-$) and MS/MS fragmentation pattern consistent with 7-O-neohesperidoside of apigenin. Although commercial rhoifolin standards exist, authentic standards for related flavonoids (rutin, astilbin, taxifolin) were used in our workflow, while rhoifolin identification relied on accurate mass and MS/MS fragmentation (MSI Level 2). Relative quantification was employed as our untargeted workflow aimed to capture variation across 368 compounds rather than absolute quantification of individual metabolites.

5.3. Statistical analysis

Data were analysed using R v4.2. Normality was tested using Shapiro-Wilk test. Correlations were calculated using Spearman's method. Network analysis was performed using Spearman correlations with $|\rho| > 0.7$ for direct rhoifolin connections and $|\rho| > 0.5$ for inter-metabolite correlations. PCA was performed on scaled, centered data using all 368 detected metabolites. Broad-sense heritability was estimated from variance components assuming 20% technical/environmental variance based on replicate variation.

CRediT authorship contribution statement

José G. Vallarino: Writing – original draft, Visualization, Validation, Methodology, Investigation, Data curation, Funding acquisition, Conceptualization. **Luca Mazzoni:** Writing – review & editing, Investigation. **Rohullah Qaderi:** Writing – review & editing, Investigation. **Franco Capocasa:** Writing – review & editing, Supervision, Methodology, Investigation. **Sonia Osorio:** Writing – review & editing, Methodology, Funding acquisition, Investigation. **Bruno Mezzetti:** Writing – review & editing, Supervision, Resources, Methodology, Investigation, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

This work was supported through funding by the European Union's

Horizon 2020 Research and Innovation Programme (BreedingValue project, grant Agreement Number 101000747), and partially by Ministerio de Ciencia e Innovación and Agencia Estatal de Investigación (PID2021-128527OB-100), and Junta de Andalucia (P21-00315). Funding for open access charge: Universidad de Málaga / CBUA.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foodchem.2026.149508.

Data availability

Complete metabolomic dataset available at DOI: 10.5281/zenodo.17483791. Raw LC-MS files available from corresponding authors upon request.

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