Horticulture Research

Horticulture Research, 2024, **11**: uhae225
https://doi.org/10.1093/hr/uhae225

Review Article

The art of tartness: the genetics of organic acid content in fresh fruits

Shixue Miao, Xiaoyu Wei, Lingcheng Zhu, Baiquan Ma and Mingjun Li*

State Key Laboratory for Crop Stress Resistance and High-Efficiency Production/Shaanxi Key Laboratory of Apple, College of Horticulture, Northwest A&F University, Yangling 712100, Shaanxi, China
*Corresponding author. E-mail: limingjun@nwsuaf.edu.cn

Abstract

Organic acids are major determinants of fruit flavor and a primary focus of fruit crop breeding. The accumulation of organic acids is determined by their synthesis, degradation, and transport, all of which are manipulated by sophisticated genetic mechanisms. Constant exploration of the genetic basis of organic acid accumulation, especially through linkage analysis, association analysis, and evolutionary analysis, have identified numerous loci in recent decades. In this review, the genetic loci and genes responsible for malate and citrate contents in fruits are discussed from the genetic perspective. Technologies such as gene transformation and genome editing as well as efficient breeding using marker-assisted selection (MAS) and genomic selection (GS) are expected to break the bottleneck of traditional fruit crop breeding and promote fruit quality improvement.

Introduction

Fresh fruits make up a large proportion of a healthful human diet. Fruit flavor is a primary factor affecting consumption behavior and has been a major focus of genetic research and breeding practices [1–3]. Sugars and organic acids determine the sweet–sour taste of fruit and thus work together to influence fruit flavor; however, sweet–sour taste perception is more affected by organic acids according to sensory evaluations [4–7]. Therefore, organic acids play a vital role in flavor improvement of fruit crops [8]. Mechanisms and regulation of organic acid accumulation in fruit crops have been well reported and reviewed [9, 10]. Nevertheless, it remains uncertain how biochemical pathway-related genes and regulation factors involved in organic acid accumulation can be applied to breeding practices. Forward genetics promotes the understanding of the genetic basis of phenotypic traits, as well as reveals natural genetic variations, which can be utilized in marker-assisted selection (MAS) to support traditional breeding and in genome engineering. Understanding of the genetics of organic acid content will aid in developing more efficient strategies for fruit crop breeding and provide more promising approaches for fruit flavor improvement.

As an important indicator of fruit flavor, the content of organic acids has been a main selection target during fruit crop domestication and improvement. Domestication syndrome traits associated with organic acid content have been broadly reported in fruit crops such as apple (*Malus domestica* Borkh.) [11], peach (*Prunus persica* L.) [2], mandarin (*Citrus reticulata* Blanco) [12], Chinese cherry (*Prunus pseudocerasus* (Lindl.) G.Don) [13], and tomato (*Solanum lycopersicum* L.) [1]. Organic acid content is a classic quantitative trait controlled by multiple genes. Quantitative trait locus (QTL) mapping, genome-wide association studies (GWAS), and evolutionary analysis in natural populations have been widely employed to explore genetic loci and variations associated with fruit organic acid content [8, 14–20]. Although endeavors in exploring the genetic basis underlying organic acids have been consistently reported, there are few available overviews on the genetic loci, genes, and corresponding mechanisms related to organic acid accumulation. In this review, progress in understanding the organic acid content of fruit crops is summarized from a genetic perspective with the hope of more efficient and precise breeding for fruit quality improvement in the near future.

Metabolism and transport of organic acids in fruits

The main organic acids in fruits are malic acid and citric acid. The predominant type of organic acid varies among species. For instance, malic acid is dominant in apple [21], peach [22], loquat (*Eriobotrya japonica* Lindl.) [23], and sweet cherry (*Prunus avium* L.) [24], while citric acid is the most abundant acid in citrus (*Citrus* spp.) [25]. Malate and citrate are technically defined as the conjugated base of malic acid and citric acid respectively; however, these two terms are generally used to describe all physiological forms of the two acids [10, 23, 26]. The consensus is that the accumulation of malate and citrate in fruit is determined by synthesis, degradation, and transport (Fig. 1).

Biosynthesis of malate relies on two key enzymes, cytosolic NAD-dependent malate dehydrogenase (NAD-cytMDH) and phosphoenolpyruvate carboxylase (PEPC). The glycolysis product phosphoenolpyruvate (PEP) is carboxylated by PEPC into oxaloacetate (OAA), and OAA can then be reduced by NAD-cytMDH to malate in the cytosol [27–30]. Malate degradation occurs in two

Received: 24 April 2024; **Accepted:** 28 July 2024; **Published:** 6 August 2024; **Corrected and Typeset:** 1 October 2024
© The Author(s) 2024. Published by Oxford University Press on behalf of Nanjing Agricultural University. This is an Open Access article distributed under the terms of the Creative Commons Attribution License (https://creativecommons.org/licenses/by/4.0/), which permits unrestricted reuse, distribution, and reproduction in any medium, provided the original work is properly cited.

Downloaded from https://academic.oup.com/hr/article/11/10/uhae225/7728139 by guest on 12 February 2026

Conclusions and perspectives

Citrate and malate are predominant organic acids in fruit crops. In terms of malate, reported genetic loci and variations are primarily focused on vacuolar transporters, particularly ALMTs, as well as transcription factors directly regulating these transporters. For citrate, there are a very limited number of genes that have been verified to contain natural variations associated with citrate content (*CitAN1* and *CitPH4* in citrus, *CmPH* in sweet melon, and *ZjACO3* in jujube). Overall, numerous loci for organic acid content have been identified in fruit crops; however, it remains challenging to identify key genes controlling this trait under these loci. The integration of multi-omics and reverse genetics holds great potential as a robust solution to address this issue. Moreover, the identification of key genes regulating fruit acidity in major fruit crops, such as *ALMT*s, facilitates the exploration of homologous genes in other fruit crops. This offers an opportunity to unravel the genetic basis underlying organic acid content in fruit crops lacking high-quality reference genomes or appropriate mapping populations.

The identification of genetic loci and genes regulating organic acids can contribute to molecular breeding and quality improvement of fruit crops. Natural mutations associated with organic acid content can be imitated and recreated by CRISPR/Cas-based genome editing (knockout, knock-in, base editing, etc.) independently of the integration of exogenous DNA fragments into the plant genome, which allows the production of transgene-free cultivars with ideal fruit acidity, thereby achieving precise improvement of fruit crops. Furthermore, with the application of cost-effective and high-throughput genotyping platforms such as SNP chips, identified genetic loci controlling organic acid content could serve MAS in breeding programs and aid in molecular design breeding of fruit crops. However, before this, the universal effectiveness and genetic contribution of these genetic loci need to be further validated in larger populations with different genetic backgrounds.

Both malate and citrate are primary metabolites originating from glycolysis. A potential association between phosphofructokinase (a rate-limiting enzyme in glycolysis) and citrate content was proposed in a QTL mapping study [78]. It is plausible that changes in glycolysis rate could influence the levels of malate and citrate since an excess or deficiency of PEP directly determines the carbon flux into acids. In addition, *MdNADP-ME* was also reported to regulate fructose content [60], indicating the interrelation of acids and sugars. Given that both sugar and acid levels have changed during the domestication process of most fruit crops, there might exist pivotal genes coordinating sugar and acid metabolism which have undergone selection and contributed to the flavor formation of fruits. Deciphering interrelation mechanisms of sugar and acid metabolism would improve the understanding of genetic regulation of organic acid accumulation.

In this review, genetic studies on organic acid content in fruit crops are summarized, providing valuable information for fruit quality improvement. The discovery of citrate tonoplast transporters is expected to facilitate the progress of the genetics of citrate content, and the further exploration of mutual regulation between organic acids and sugars would provide new insights into fruit acidity and flavor formation.

Acknowledgements

This work was supported by the Shaanxi Science and Technology Innovation Team Project (2022TD-12) and the Young Elite Scientists Sponsorship Program by CAST (2023QNRC001).

Author contributions

S.M. and M.L. conceived this review. S.M. wrote original draft. X.W., L.Z., B.M., and M.L. revised the manuscript. All authors approved the final manuscript.

Data availability statement

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

Conflict of interests

The authors declare no conflict of interest.

Supplementary data

Supplementary data are available at *Horticulture Research* online.

References

1. Zhao J, Sauvage C, Zhao J. *et al.* Meta-analysis of genome-wide association studies provides insights into genetic control of tomato flavor. *Nat Commun.* 2019;**10**:1534
2. Li Y, Cao K, Zhu G. *et al.* Genomic analyses of an extensive collection of wild and cultivated accessions provide new insights into peach breeding history. *Genome Biol.* 2019;**20**:36
3. Lin Q, Chen J, Liu X. *et al.* A metabolic perspective of selection for fruit quality related to apple domestication and improvement. *Genome Biol.* 2023;**24**:95
4. Baccichet I, Tagliabue GA, Da Silva LC. *et al.* Sensory perception of citrate and malate and their impact on the overall taste in apricot (*Prunus armeniaca* L.) fruits. *Sci Hortic.* 2023;**321**:112266
5. Drkenda P, Ćulah A, Spaho N. *et al.* How do consumers receive sensory attributes of apple? *Food Secur.* 2021;**10**:2667
6. Colaric M, Veberic R, Stampar F. *et al.* Evaluation of peach and nectarine fruit quality and correlations between sensory and chemical attributes. *J Sci Food Agric.* 2005;**85**:2611–6
7. Esti M, Messia MC, Sinesio F. *et al.* Quality evaluation of peaches and nectarines by electrochemical and multivariate analyses: relationships between analytical measurements and sensory attributes. *Food Chem.* 1997;**60**:659–66
8. Liebhard R, Kellerhals M, Pfammatter W. *et al.* Mapping quantitative physiological traits in apple (*Malus* × *domestica* Borkh.). *Plant Mol Biol.* 2003;**52**:511–26
9. Huang X-Y, Wang C-K, Zhao Y-W. *et al.* Mechanisms and regulation of organic acid accumulation in plant vacuoles. *Hortic Res.* 2021;**8**:227
10. Etienne A, Génard M, Lobit P. *et al.* What controls fleshy fruit acidity? A review of malate and citrate accumulation in fruit cells. *J Exp Bot.* 2013;**64**:1451–69
11. Ma B, Chen J, Zheng H. *et al.* Comparative assessment of sugar and malic acid composition in cultivated and wild apples. *Food Chem.* 2015;**172**:86–91
12. Wang L, He F, Huang Y. *et al.* Genome of wild mandarin and domestication history of mandarin. *Mol Plant.* 2018;**11**:1024–37
13. Zhou J, Yang S, Ma Y. *et al.* Soluble sugar and organic acid composition and flavor evaluation of Chinese cherry fruits. *Food Chem X.* 2023;**20**:100953
14. Xu K, Wang A, Brown S. Genetic characterization of the *Ma* locus with pH and titratable acidity in apple. *Mol Breeding.* 2012;**30**:899–912
15. Ma B, Zhao S, Wu B. *et al.* Construction of a high density linkage map and its application in the identification of QTLs

Downloaded from https://academic.oup.com/hr/article/11/10/uhae225/7728139 by guest on 12 February 2026

for soluble sugar and organic acid components in apple. *Tree Genet Genomes*. 2016;**12**:1
16. Jia D, Shen F, Wang Y. *et al.* Apple fruit acidity is genetically diversified by natural variations in three hierarchical epistatic genes: *MdSAUR37*, *MdPP2CH* and *MdALMTII*. *Plant J*. 2018;**95**:427–43
17. Cao K, Zhou Z, Wang Q. *et al.* Genome-wide association study of 12 agronomic traits in peach. *Nat Commun*. 2016;**7**:13246
18. Zhang M-Y, Xue C, Hu H. *et al.* Genome-wide association studies provide insights into the genetic determination of fruit traits of pear. *Nat Commun*. 2021;**12**:1144
19. Liao L, Zhang W, Zhang B. *et al.* Unraveling a genetic roadmap for improved taste in the domesticated apple. *Mol Plant*. 2021;**14**:1454–71
20. Wang Q, Cao K, Cheng L. *et al.* Multi-omics approaches identify a key gene, *PpTST1*, for organic acid accumulation in peach. *Hortic Res*. 2022;**9**:uhac026
21. Yamaki S. Isolation of vacuoles from immature apple fruit flesh and compartmentation of sugars, organic acids, phenolic compounds and amino acids. *Plant Cell Physiol*. 1984;**25**:151–66
22. Moing A, Svanella L, Rolin D. *et al.* Compositional changes during the fruit development of two peach cultivars differing in juice acidity. *J Am Soc Hortic Sci*. 1998;**123**:770–5
23. Deng H, Li X, Wang Y. *et al.* Organic acid accumulation and associated dynamic changes in enzyme activity and gene expression during fruit development and ripening of common loquat and its interspecific hybrid. *Food Secur*. 2023;**12**:911
24. Usenik V, Fabčič J, Štampar F. Sugars, organic acids, phenolic composition and antioxidant activity of sweet cherry (*Prunus avium* L.). *Food Chem*. 2008;**107**:185–92
25. Yamaki YT. Organic acids in the juice of citrus fruits. *J Jpn Soc Hortic Sci*. 1989;**58**:587–94
26. Sweetman C, Deluc LG, Cramer GR. *et al.* Regulation of malate metabolism in grape berry and other developing fruits. *Phytochemistry*. 2009;**70**:1329–44
27. Miller SS, Driscoll BT, Gregerson RG. *et al.* Alfalfa malate dehydrogenase (MDH): molecular cloning and characterization of five different forms reveals a unique nodule-enhanced MDH. *Plant J*. 1998;**15**:173–84
28. Diakou P, Svanella L, Raymond P. *et al.* Phosphoenolpyruvate carboxylase during grape berry development: protein level, enzyme activity and regulation. *Funct Plant Biol*. 2000;**27**:221
29. Yao Y-X, Li M, Zhai H. *et al.* Isolation and characterization of an apple cytosolic malate dehydrogenase gene reveal its function in malate synthesis. *J Plant Physiol*. 2011;**168**:474–80
30. Caburatan L, Park J. Differential expression, tissue-specific distribution, and posttranslational controls of phosphoenolpyruvate carboxylase. *Plants (Basel)*. 2021;**10**:1887
31. Leegood RC, Walker RP. Regulation and roles of phosphoenolpyruvate carboxykinase in plants. *Arch Biochem Biophys*. 2003;**414**:204–10
32. Famiani F, Cultrera NGM, Battistelli A. *et al.* Phosphoenolpyruvate carboxykinase and its potential role in the catabolism of organic acids in the flesh of soft fruit during ripening. *J Exp Bot*. 2005;**56**:2959–69
33. Yao Y-X, Li M, Liu Z. *et al.* Molecular cloning of three malic acid related genes *MdPEPC*, *MdVHA-A*, *MdcyME* and their expression analysis in apple fruits. *Sci Hortic*. 2009;**122**:404–8
34. Sadka A, Dahan E, Cohen L. *et al.* Aconitase activity and expression during the development of lemon fruit. *Physiol Plant*. 2000;**108**:255–62
35. Lin Q, Wang C, Dong W. *et al.* Transcriptome and metabolome analyses of sugar and organic acid metabolism in ponkan (*Citrus reticulata*) fruit during fruit maturation. *Gene*. 2015;**554**:64–74
36. Zhu L, Li B, Wu L. *et al.* MdERDL6-mediated glucose efflux to the cytosol promotes sugar accumulation in the vacuole through up-regulating TSTs in apple and tomato. *Proc Natl Acad Sci USA*. 2021;**118**:e2022788118
37. Zhu L, Li Y, Wang C. *et al.* The SnRK2.3-AREB1-TST1/2 cascade activated by cytosolic glucose regulates sugar accumulation across tonoplasts in apple and tomato. *Nat Plants*. 2023;**9**:951–64
38. Liu Z, Mao Z, Li M. *et al.* Vacuole: a repository to control fruit flavor quality. *Fruit Res*. 2023;**3**:12
39. Ye J, Wang X, Hu T. *et al.* An InDel in the promoter of *Al-ACTIVATED MALATE TRANSPORTER9* selected during tomato domestication determines fruit malate contents and aluminum tolerance. *Plant Cell*. 2017;**29**:2249–68
40. Bai Y, Dougherty L, Li M. *et al.* A natural mutation-led truncation in one of the two aluminum-activated malate transporter-like genes at the *Ma* locus is associated with low fruit acidity in apple. *Mol Gen Genomics*. 2012;**287**:663–78
41. Li C, Dougherty L, Coluccio AE. *et al.* Apple ALMT9 requires a conserved C-terminal domain for malate transport underlying fruit acidity. *Plant Physiol*. 2020;**182**:992–1006
42. De Angeli A, Baetz U, Francisco R. *et al.* The vacuolar channel VvALMT9 mediates malate and tartrate accumulation in berries of *Vitis vinifera*. *Planta*. 2013;**238**:283–91
43. Alabd A, Cheng H, Ahmad M. *et al.* ABRE-BINDING FACTOR3-WRKY DNA-BINDING PROTEIN44 module promotes salinity-induced malate accumulation in pear. *Plant Physiol*. 2023;**192**:1982–96
44. Fu B, Wang W, Li X. *et al.* A dramatic decline in fruit citrate induced by mutagenesis of a NAC transcription factor, AcNAC1. *Plant Biotechnol J*. 2023;**21**:1695–706
45. Liu S, Liu X, Gou B. *et al.* The interaction between CitMYB52 and CitbHLH2 negatively regulates citrate accumulation by activating CitALMT in citrus fruit. *Front Plant Sci*. 2022;**13**:848869
46. Hurth MA, Suh SJ, Kretzschmar T. *et al.* Impaired pH homeostasis in *Arabidopsis* lacking the vacuolar dicarboxylate transporter and analysis of carboxylic acid transport across the tonoplast. *Plant Physiol*. 2005;**137**:901–10
47. Yao Y-X, Dong Q-L, You C-X. *et al.* Expression analysis and functional characterization of apple *MdVHP1* gene reveals its involvement in Na^+, malate and soluble sugar accumulation. *Plant Physiol Biochem*. 2011;**49**:1201–8
48. Shimada T, Nakano R, Shulaev V. *et al.* Vacuolar citrate/H^+ symporter of citrus juice cells. *Planta*. 2006;**224**:472–80
49. Maliepaard C, Alston FH, Van Arkel G. *et al.* Aligning male and female linkage maps of apple (*Malus pumila* Mill.) using multi-allelic markers. *Theor Appl Genet*. 1998;**97**:60–73
50. Kenis K, Keulemans J, Davey MW. Identification and stability of QTLs for fruit quality traits in apple. *Tree Genet Genomes*. 2008;**4**:647–61
51. Khan SA, Beekwilder J, Schaart JG. *et al.* Differences in acidity of apples are probably mainly caused by a malic acid transporter gene on LG16. *Tree Genet Genomes*. 2013;**9**:475–87
52. Verma S, Evans K, Guan Y. *et al.* Two large-effect QTLs, *Ma* and *Ma3*, determine genetic potential for acidity in apple fruit: breeding insights from a multi-family study. *Tree Genet Genomes*. 2019;**15**:18
53. Rymenants M, Van De Weg E, Auwerkerken A. *et al.* Detection of QTL for apple fruit acidity and sweetness using sensorial evaluation in multiple pedigreed full-sib families. *Tree Genet Genomes*. 2020;**16**:71

Downloaded from https://academic.oup.com/hr/article/11/10/uhae225/7728139 by guest on 12 February 2026

54. Peng Y, Yuan Y, Chang W. *et al.* Transcriptional repression of *MdMa1* by MdMYB21 in *Ma* locus decreases malic acid content in apple fruit. *Plant J.* 2023;**115**:1231–42
55. Zhang Q, Ma B, Li H. *et al.* Identification, characterization, and utilization of genome-wide simple sequence repeats to identify a QTL for acidity in apple. *BMC Genomics.* 2012;**13**:537
56. Sun R, Chang Y, Yang F. *et al.* A dense SNP genetic map constructed using restriction site-associated DNA sequencing enables detection of QTLs controlling apple fruit quality. *BMC Genomics.* 2015;**16**:747
57. Jia D, Wu P, Shen F. *et al.* Genetic variation in the promoter of an R2R3–MYB transcription factor determines fruit malate content in apple (*Malus domestica* Borkh.). *Plant Physiol.* 2021;**186**: 549–68
58. Ban S, Xu K. Identification of two QTLs associated with high fruit acidity in apple using pooled genome sequencing analysis. *Hortic Res.* 2020;**7**:171
59. Gao M, Yang N, Shao Y. *et al.* An insertion in the promoter of a malate dehydrogenase gene regulates malic acid content in apple fruit. *Plant Physiol.* 2024;kiae303
60. Fu W, Zhao L, Qiu W. *et al.* Whole-genome resequencing identifies candidate genes and allelic variation in the *MdNADP-ME* promoter that regulate fruit malate and fructose contents in apple. *Plant Commun.* 2024;**100973**:
61. Kumar S, Molloy C, Hunt M. *et al.* GWAS provides new insights into the genetic mechanisms of phytochemicals production and red skin colour in apple. *Hortic Res.* 2022;**9**:uhac218
62. Duan N, Bai Y, Sun H. *et al.* Genome re-sequencing reveals the history of apple and supports a two-stage model for fruit enlargement. *Nat Commun.* 2017;**8**:249
63. Sun X, Jiao C, Schwaninger H. *et al.* Phased diploid genome assemblies and pan-genomes provide insights into the genetic history of apple domestication. *Nat Genet.* 2020;**52**:1423–32
64. Ma B, Liao L, Fang T. *et al.* A *Ma10* gene encoding P-type ATPase is involved in fruit organic acid accumulation in apple. *Plant Biotechnol J.* 2019;**17**:674–86
65. Zheng L, Liao L, Duan C. *et al.* Allelic variation of *MdMYB123* controls malic acid content by regulating *MdMa1* and *MdMa11* expression in apple. *Plant Physiol.* 2023;**192**:1877–91
66. Velasco R, Zharkikh A, Affourtit J. *et al.* The genome of the domesticated apple (*Malus* × *domestica* Borkh.). *Nat Genet.* 2010;**42**:833–9
67. Li C, Krishnan S, Zhang M. *et al.* Alternative splicing underpins the ALMT9 transporter function for vacuolar malic acid accumulation in apple. *Adv Sci.* 2024;**11**:e2310159
68. Canel C, Bailey-Serres JN, Roose ML. In vitro [^{14}C]citrate uptake by tonoplast vesicles of acidless citrus juice cells. *J Am Soc Hortic Sci.* 1995;**120**:510–4
69. Strazzer P, Spelt CE, Li S. *et al.* Hyperacidification of citrus fruits by a vacuolar proton-pumping P-ATPase complex. *Nat Commun.* 2019;**10**:744
70. He J, Xu Y, Huang D. *et al.* TRIPTYCHON-LIKE regulates aspects of both fruit flavor and color in citrus. *J Exp Bot.* 2022;**73**:3610–24
71. Verweij W, Spelt C, Di Sansebastiano G-P. *et al.* An H^+ P-ATPase on the tonoplast determines vacuolar pH and flower colour. *Nat Cell Biol.* 2008;**10**:1456–62
72. Faraco M, Spelt C, Bliek M. *et al.* Hyperacidification of vacuoles by the combined action of two different P-ATPases in the tonoplast determines flower color. *Cell Rep.* 2014;**6**:32–43
73. Quattrocchio F, Verweij W, Kroon A. *et al.* PH4 of petunia is an R2R3 MYB protein that activates vacuolar acidification through interactions with basic-helix-loop-helix transcription factors of the anthocyanin pathway. *Plant Cell.* 2006;**18**:1274–91
74. Butelli E, Licciardello C, Ramadugu C. *et al.* Noemi controls production of flavonoid pigments and fruit acidity and illustrates the domestication routes of modern citrus varieties. *Curr Biol.* 2019;**29**:158–164.e2
75. Huang Y, He J, Xu Y. *et al.* Pangenome analysis provides insight into the evolution of the orange subfamily and a key gene for citric acid accumulation in citrus fruits. *Nat Genet.* 2023;**55**: 1964–75
76. Wu GA, Terol J, Ibanez V. *et al.* Genomics of the origin and evolution of citrus. *Nature.* 2018;**554**:311–6
77. Minamikawa MF, Nonaka K, Kaminuma E. *et al.* Genome-wide association study and genomic prediction in citrus: potential of genomics-assisted breeding for fruit quality traits. *Sci Rep.* 2017;**7**:4721
78. Khefifi H, Dumont D, Costantino G. *et al.* Mapping of QTLs for citrus quality traits throughout the fruit maturation process on clementine (*Citrus reticulata* × *C. sinensis*) and mandarin (*C. reticulata* Blanco) genetic maps. *Tree Genet Genomes.* 2022;**18**:40
79. Lu X, Cao X, Li F. *et al.* Comparative transcriptome analysis reveals a global insight into molecular processes regulating citrate accumulation in sweet orange (*Citrus sinensis*). *Physiol Plant.* 2016;**158**:463–82
80. Asins MJ, Raga V, Bernet GP. *et al.* Genetic analysis of reproductive, vegetative and fruit quality traits to improve citrus varieties. *Tree Genet Genomes.* 2015;**11**:117
81. Yu Y, Chen C, Gmitter FG. QTL mapping of mandarin (*Citrus reticulata*) fruit characters using high-throughput SNP markers. *Tree Genet Genomes.* 2016;**12**:77
82. Curtolo M, Cristofani-Yaly M, Gazaffi R. *et al.* QTL mapping for fruit quality in citrus using DArTseq markers. *BMC Genomics.* 2017;**18**:289
83. Bastías A, López-Climent M, Valcárcel M. *et al.* Modulation of organic acids and sugar content in tomato fruits by an abscisic acid-regulated transcription factor. *Physiol Plant.* 2011;**141**:215–26
84. Schauer N, Zamir D, Fernie AR. Metabolic profiling of leaves and fruit of wild species tomato: a survey of the *Solanum lycopersicum* complex. *J Exp Bot.* 2004;**56**:297–307
85. Sauvage C, Segura V, Bauchet G. *et al.* Genome-wide association in tomato reveals 44 candidate loci for fruit metabolic traits. *Plant Physiol.* 2014;**165**:1120–32
86. Tieman D, Zhu G, Resende MFR. *et al.* A chemical genetic roadmap to improved tomato flavor. *Science.* 2017;**355**:391–4
87. Bauchet G, Grenier S, Samson N. *et al.* Identification of major loci and genomic regions controlling acid and volatile content in tomato fruit: implications for flavor improvement. *New Phytol.* 2017;**215**:624–41
88. Gai W, Yang F, Yuan L. *et al.* Multiple-model GWAS identifies optimal allelic combinations of quantitative trait loci for malic acid in tomato. *Hortic Res.* 2023;**10**:uhad021
89. Razifard H, Ramos A, Della Valle AL. *et al.* Genomic evidence for complex domestication history of the cultivated tomato in Latin America. *Mol Biol Evol.* 2020;**37**:1118–32
90. Gai W, Yuan L, Yang F. *et al.* Genome-wide variants and optimal allelic combinations for citric acid in tomato. *Hortic Res.* 2024;**11**:uhae070
91. Ruggieri V, Francese G, Sacco A. *et al.* An association mapping approach to identify favourable alleles for tomato fruit quality breeding. *BMC Plant Biol.* 2014;**14**:337
92. Zhao J, Xu Y, Ding Q. *et al.* Association mapping of main tomato fruit sugars and organic acids. *Front Plant Sci.* 2016;**7**:1286
93. Çolak NG, Eken NT, Ülger M. *et al.* Exploring wild alleles from *Solanum pimpinellifolium* with the potential to improve tomato flavor compounds. *Plant Sci.* 2020;**298**:110567

Downloaded from https://academic.oup.com/hr/article/11/10/uhae225/7728139 by guest on 12 February 2026

94. Fulton TM, Bucheli P, Voirol E. *et al.* Quantitative trait loci (QTL) affecting sugars, organic acids and other biochemical properties possibly contributing to flavor, identified in four advanced backcross populations of tomato. *Euphytica*. 2002;**127**:163–77
95. Toubiana D, Semel Y, Tohge T. *et al.* Metabolic profiling of a mapping population exposes new insights in the regulation of seed metabolism and seed, fruit, and plant relations. *PLoS Genet*. 2012;**8**:e1002612
96. Causse M, Duffe P, Gomez MC. *et al.* A genetic map of candidate genes and QTLs involved in tomato fruit size and composition. *J Exp Bot*. 2004;**55**:1671–85
97. Capel C, Fernández Del Carmen A, Alba JM. *et al.* Wide-genome QTL mapping of fruit quality traits in a tomato RIL population derived from the wild-relative species *Solanum pimpinellifolium* L. *Theor Appl Genet*. 2015;**128**:2019–35
98. Tieman DM, Zeigler M, Schmelz EA. *et al.* Identification of loci affecting flavour volatile emissions in tomato fruits. *J Exp Bot*. 2006;**57**:887–96
99. Schauer N, Semel Y, Roessner U. *et al.* Comprehensive metabolic profiling and phenotyping of interspecific introgression lines for tomato improvement. *Nat Biotechnol*. 2006;**24**:447–54
100. Wang L, Jiang X, Zhao L. *et al.* A candidate *PpRPH* gene of the *D* locus controlling fruit acidity in peach. *Plant Mol Biol*. 2021;**105**:321–32
101. Yu Y, Guan J, Xu Y. *et al.* Population-scale peach genome analyses unravel selection patterns and biochemical basis underlying fruit flavor. *Nat Commun*. 2021;**12**:3604
102. Reshef N, Karn A, Manns DC. *et al.* Stable QTL for malate levels in ripe fruit and their transferability across *Vitis* species. *Hortic Res*. 2022;**9**:uhac009
103. Bayo-Canha A, Costantini L, Fernández-Fernández JI. *et al.* QTLs related to berry acidity identified in a wine grapevine population grown in warm weather. *Plant Mol Biol Rep*. 2019;**37**:157–69
104. Alahakoon D, Fennell A, Helget Z. *et al.* Berry anthocyanin, acid, and volatile trait analyses in a grapevine-interspecific F2 population using an integrated GBS and rhAmpSeq genetic map. *Plants (Basel)*. 2022;**11**:696
105. Wu J, Wang Y, Xu J. *et al.* Diversification and independent domestication of Asian and European pears. *Genome Biol*. 2018;**19**:77
106. Cohen S, Itkin M, Yeselson Y. *et al.* The *PH* gene determines fruit acidity and contributes to the evolution of sweet melons. *Nat Commun*. 2014;**5**:4026
107. Zhao G, Lian Q, Zhang Z. *et al.* A comprehensive genome variation map of melon identifies multiple domestication events and loci influencing agronomic traits. *Nat Genet*. 2019;**51**:1607–15
108. Zhang C, Geng Y, Liu H. *et al.* Low-acidity *ALUMINUM-DEPENDENT MALATE TRANSPORTER4* genotype determines malate content in cultivated jujube. *Plant Physiol*. 2023;**191**:414–27
109. Liu H, Zhao X, Bi J. *et al.* A natural mutation in the promoter of the aconitase gene *ZjACO3* influences fruit citric acid content in jujube. *Hortic Res*. 2024;**11**:uhae003
110. Burger Y, Sa'ar U, Distelfeld A. *et al.* Development of sweet melon (*Cucumis melo*) genotypes combining high sucrose and organic acid content. *J Am Soc Hortic Sci*. 2003;**128**:537–40
111. Li M, Su J, Yang H. *et al.* Grape tartaric acid: chemistry, function, metabolism, and regulation. *Horticulturae*. 2023;**9**:1173
112. Houel C, Chatbanyong R, Doligez A. *et al.* Identification of stable QTLs for vegetative and reproductive traits in the microvine (*Vitis vinifera* L.) using the 18 K Infinium chip. *BMC Plant Biol*. 2015;**15**:205
113. Duchêne É, Dumas V, Butterlin G. *et al.* Genetic variations of acidity in grape berries are controlled by the interplay between organic acids and potassium. *Theor Appl Genet*. 2020;**133**:993–1008
114. Negus KL, Chen L-L, Fresnedo-Ramírez J. *et al.* Identification of QTLs for berry acid and tannin in a *Vitis aestivalis*-derived 'Norton'-based population. *Fruit Res*. 2021;**1**:8
115. Dirlewanger E, Pronier V, Parvery C. *et al.* Genetic linkage map of peach [*Prunus persica* (L.) Batsch] using morphological and molecular markers. *Theor Appl Genet*. 1998;**97**:888–95
116. Dirlewanger E, Moing A, Rothan C. *et al.* Mapping QTLs controlling fruit quality in peach (*Prunus persica* (L.) Batsch). *Theor Appl Genet*. 1999;**98**:18–31
117. Etienne C, Rothan C, Moing A. *et al.* Candidate genes and QTLs for sugar and organic acid content in peach [*Prunus persica* (L.) Batsch]. *Theor Appl Genet*. 2002;**105**:145–59
118. Dirlewanger E, Cosson P, Boudehri K. *et al.* Development of a second-generation genetic linkage map for peach [*Prunus persica* (L.) Batsch] and characterization of morphological traits affecting flower and fruit. *Tree Genet Genomes*. 2006;**3**:1–13
119. Boudehri K, Bendahmane A, Cardinet G. *et al.* Phenotypic and fine genetic characterization of the *D* locus controlling fruit acidity in peach. *BMC Plant Biol*. 2009;**9**:59
120. Eduardo I, López-Girona E, Batlle I. *et al.* Development of diagnostic markers for selection of the subacid trait in peach. *Tree Genet Genomes*. 2014;**10**:1695–709
121. Hickey LT, Hafeez AN, Robinson H. *et al.* Breeding crops to feed 10 billion. *Nat Biotechnol*. 2019;**37**:744–54
122. Chagné D, Vanderzande S, Kirk C. *et al.* Validation of SNP markers for fruit quality and disease resistance loci in apple (*Malus* × *domestica* Borkh.) using the OpenArray® platform. *Hortic Res*. 2019;**6**:30
123. Kumar S, Garrick DJ, Bink MC. *et al.* Novel genomic approaches unravel genetic architecture of complex traits in apple. *BMC Genomics*. 2013;**14**:393
124. Alemu A, Åstrand J, Montesinos-López OA. *et al.* Genomic selection in plant breeding: key factors shaping two decades of progress. *Mol Plant*. 2024;**17**:552–78
125. Kumar S, Chagné D, Bink MCAM. *et al.* Genomic selection for fruit quality traits in apple (*Malus* × *domestica* Borkh.). *PLoS One*. 2012;**7**:e36674
126. Kostick SA, Bernardo R, Luby JJ. Genomewide selection for fruit quality traits in apple: breeding insights gained from prediction and postdiction. *Hortic Res*. 2023;**10**:uhad088
127. Chen K, Wang Y, Zhang R. *et al.* CRISPR/Cas genome editing and precision plant breeding in agriculture. *Annu Rev Plant Biol*. 2019;**70**:667–97
128. Gao C. Genome engineering for crop improvement and future agriculture. *Cell*. 2021;**184**:1621–35
129. Holme IB, Gregersen PL, Brinch-Pedersen H. Induced genetic variation in crop plants by random or targeted mutagenesis: convergence and differences. *Front Plant Sci*. 2019;**10**:1468
130. Zsögön A, Cermak T, Voytas D. *et al.* Genome editing as a tool to achieve the crop ideotype and de novo domestication of wild relatives: case study in tomato. *Plant Sci*. 2017;**256**:120–30
131. Li T, Yang X, Yu Y. *et al.* Domestication of wild tomato is accelerated by genome editing. *Nat Biotechnol*. 2018;**36**:1160–3
132. Zsögön A, Čermák T, Naves ER. *et al.* De novo domestication of wild tomato using genome editing. *Nat Biotechnol*. 2018;**36**:1211–6

Downloaded from https://academic.oup.com/hr/article/11/10/uhae225/7728139 by guest on 12 February 2026