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Humaira Nabi

M.Sc., Division of Fruit Science,
Sher-e-Kashmir University of
Agricultural Sciences and
Technology of Kashmir (SKUAST-
K), Faculty of Horticulture,
Shalimar, Srinagar, Jammu &
Kashmir, India

Ashaq Hussain Pandit

Assistant Professor, Division of
Fruit Science, Sher-e-Kashmir
University of Agricultural Sciences
and Technology of Kashmir
(SKUAST-K), Faculty of
Horticulture, Shalimar, Srinagar,
Jammu & Kashmir, India

Abdul Raouf Malik

Assistant Professor, Division of
Fruit Science, Sher-e-Kashmir
University of Agricultural Sciences
and Technology of Kashmir
(SKUAST-K), Faculty of
Horticulture, Shalimar, Srinagar,
Jammu & Kashmir, India.

Gazala Mansoor

Ph.D. Scholar, Division of Fruit
Science, Sher-e-Kashmir University
of Agricultural Sciences and
Technology of Kashmir (SKUAST-
K), Faculty of Horticulture,
Shalimar, Srinagar, Jammu &
Kashmir, India

Rafiya Mushtaq Zargar

Horticulture Development Officer,
Agriculture & Horticulture
Development Department (ACHD),
Rajbagh, Srinagar, Jammu &
Kashmir, India

Corresponding Author:**Ashaq Hussain Pandit**

Assistant Professor, Division of
Fruit Science, Sher-e-Kashmir
University of Agricultural Sciences
and Technology of Kashmir
(SKUAST-K), Faculty of
Horticulture, Shalimar, Srinagar,
Jammu & Kashmir, India

Genetic and epigenetic regulation of apple fruit quality traits: Molecular mechanisms and breeding perspectives

Humaira Nabi, Ashaq Hussain Pandit, Abdul Raouf Malik, Gazala Mansoor and Rafiya Mushtaq Zargar

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Abstract

Apple is one of the most widely cultivated fruit crops globally, and fruit quality attributes such as color, size, shape, flavor, acidity, firmness, and storability are critical determinants of consumer preference and market value. These traits are typically quantitative in nature and are controlled by complex interactions among multiple genes and environmental factors. Recent advances in molecular biology, genomics, and epigenomics have significantly improved our understanding of the genetic and epigenetic mechanisms underlying apple fruit quality traits. This review summarizes current knowledge on the genetic architecture and epigenetic regulation of major apple fruit quality characteristics. Key genes and quantitative trait loci (QTLs) controlling fruit color, size, shape, aroma, acidity, storage behavior, and ripening are discussed, including the role of transcription factors, hormone signaling pathways, and metabolic genes. Particular emphasis is placed on the role of epigenetic modifications such as DNA methylation, histone modifications, and small RNAs in regulating gene expression involved in anthocyanin biosynthesis, ethylene production, and fruit development. Emerging genomic approaches including genome-wide association studies (GWAS), next-generation sequencing, and transcriptomic analyses have facilitated the identification of candidate genes and regulatory networks governing fruit quality. Understanding the interplay between genetic and epigenetic mechanisms provides new opportunities for improving apple fruit quality through molecular breeding and genomics-assisted selection. This knowledge will contribute to the development of superior apple cultivars with enhanced quality, improved storability, and greater consumer acceptance.

Keywords: Apple fruit quality, genetic regulation, epigenetic modification, DNA methylation, quantitative trait loci (QTLs), molecular breeding

Introduction

Apple is an economically important fruit with world production of 97 million tonnes in 2023. Apple fruit quality plays a crucial role in consumer satisfaction, influencing attributes such as taste, texture, color, firmness, and shelf life. It is determined by a number of traits, which are quantitative controlled by minor polygenes or oligogenes (Zheng *et al.*, 2020) [45]. The inheritance of minor genes is affected by the environment and gene interactions. The study of genetics and epigenetics has become increasingly important in recent years as a means of understanding the fundamental processes that control fruit quality. Genetics is the study of how traits are passed down through DNA, with certain genes governing the development of different fruit features such as apple color being affected mainly by MYB TFs, ripening by Md ACO, Md ACS etc.

However, epigenetics deals with variations in phenotypic or gene expression that are impacted by environmental elements including soil, climate, and farming methods but do not modify the underlying DNA sequence. Histone acetylation, a well-studied post-translational modification, is an epigenetic modification that occurs in the nitrogen (N)-terminal tails of histone H3 and H4 (Guan and Chen, 2007) [17]; it is regulated by histone acetyltransferases (HATs) and histone deacetylases (HDACs) (Verdone *et al.*, 2005) [36].

This review focuses on the genetic variation characteristics and the epigenetic perspectives of important fruit quality traits in apple.

Apple fruit quality

Quality of fruits has been defined as a dynamic synthesis of the physicochemical properties and their relation to consumer perception (Kyriacou and Roupael, 2018) [22]. Most of the fruit quality traits are polygenic (Iglesias *et al.*, 2012) [18]. Definitions of quality frequently distinguish between intrinsic qualities that are inherent to the nature of the products and determined by genotypic, agro environmental, and postharvest factors and extrinsic qualities that are impacted by socioeconomic and marketing factors that shape consumer perception of the products. Apple fruit quality is mainly determined by a set of external and internal traits and the most common worldwide external and internal traits include color, shape, size, texture, firmness, acidity, total sugars etc. These factors are determined by a number of genetic and epigenetic factors (Kingston, 1992; Shewfelt, 1999) [21, 30].

Genetics and epigenetics of apple fruit quality traits

Fruit color

Apple fruit color is mainly divided into skin color and flesh color. The skin color can be subdivided into presence or absence of red pigmentation, striped red, or blushed red. The flesh color is mainly subdivided into red fleshed and non-red fleshed. Red fleshed are further divided into type I and type II, due to differences in pigmentation patterns. In type 1, red pigmentation is observed from the fruit set through to maturity, exhibiting red fruit skin, leaves, stems, roots, and flowers. In type 2, red pigmentation is only present in the fruit cortex at the late stage of fruit development and the leaves are green (Change, 2013 and volz, 2009) [47]. The red coloration of the skin of an apple fruit is mainly attributed to anthocyanins, which are color producing secondary metabolites. So, the genes associated in the anthocyanin biosynthesis pathway are majorly linked to apple coloration. Mainly the MYB TFs are responsible for producing color in apple. The major gene MdMYB1 was the first gene identified to control the presence or absence of red pigmentation in the skin (Talos *et al.*, 2006) [32]. Two apple MYB transcription factors, MdMYB1 and MdMYB10, were reported to be responsible for apple skin or cortex coloration (Talos *et al.* 2006; Espley *et al.* 2006) [32]. GWAS analysis using single-nucleotide polymorphism (SNP) markers confirmed the association between fruit color and the MdMYB1 locus on chromosome 9 Migicovsky *et al.*, 2016; McClure *et al.*, 2019) [26, 27]. Apples that have MdMYB1-1 will exhibit a red-skinned phenotype, whereas those that do not have the MdMYB1-1 allele will have yellow or green skin (Talos *et al.*, 2006) [32]. MYB TFs, especially those encoded by MdMYB1, MdMYBA, and MdMYB10 genes, play important roles in the regulation of apple skin color (Talos, 2006; Ban, 2007; Espley, 2007) [3, 16]. However, a number of other MYB family genes also control the anthocyanin biosynthesis pathway, such as the MdMYB3, MdMYB9, MdMYB11, MdMYB12, MdMYB16, MdMYB22, MdMYBDL1, MdMYB111, and MdMYB308.

Next-generation sequencing (NGS) technologies have greatly facilitated the discovery of CNVs (Varshney, 2009) [35]. In total, 876 CNVs accounting for 3.5% of the apple genome were identified. Notably, some MYB TFs were found to have CNVs that could be linked to apple fruit coloration. It has been found that, a rearrangement in the upstream regulatory region of the gene encoding the

MdMYB10 include a series of multiple repeats, forming a microsatellite-like structure, featuring five direct tandem repeats of a 23 bp sequence. This MdMYB10 rearrangement was only present in red-fleshed apple varieties and was not observed in white-fleshed varieties (Espley, 2009) [48].

TEs accounting for 60% of the apple genome affect the appearance of some genetic variation in the color (Daccord *et al.*, 2017 and Telias *et al.*, 2011) [10, 34]. Comparative genomics analysis of 148 apple populations and a segregated hybrid population revealed that a gypsy-like long terminal repeat retrotransposon (designated red TE) was inserted 3297 bp upstream of MdMYB1, thereby activating the expression of MdMYB1 and controlling the redness of the skin (Zhang *et al.*, 2019) [44]. The red TE controlled the development of red coloration by lowering the threshold of light response.

The colour patterns of the fruit over color, such as flushed red and striped red, are mostly linked to methylation modification, which is a form of epigenetic inheritance, as compared with the presence or absence of red pigmentation in the fruit ground colour. Variations in the methylation levels of the MdMYB10 promoter can account for the variations in anthocyanin levels between the red and green stripes (Telias *et al.*, 2011) [34]. Using the striped red or blushed red fruit of the Fuji apple as the study material, thorough methylation modification investigations revealed that Argonaute 4 (MdAGO4s) methylated the MdMYB1 promoter, controlling the biosynthesis of anthocyanins (Jiang *et al.*, 2020) [20]. Hypomethylation in the MdMYB1 results in the red pigmentation of the Granny smith apple (Ma *et al.*, 2018) [25].

Small RNAs (sRNAs) have been identified as key genetic and epigenetic regulators, being involved in histone methylation and DNA modification and in apple, miR828 and miR858 regulate a large number of MYB genes through targeting the region encoding the conserved R3 domain of the MYB protein (Xia *et al.*, 2012) [41]. MiR828 triggered the targeting of MYB genes to produce secondary phased siRNAs (phased siRNAs), thereby enhancing its silencing effect.

Apple fruit weight

Apple fruit weight is an economically important factor in determining the consumer satisfaction and market value of the fruit and is a quantitative indicator of apple fruit size. It is a quantitative trait controlled by multiple genes. More than 100 QTLs associated with fruit weight have been located which include major and minor gene loci distributed on almost all the 17 chromosomes. An auxin signaling-related gene, *ARF106*, was identified to be co-localized with two QTLs associated with fruit size (Devoghalaere *et al.*, 2012) [11]. In a transcriptomic study of "Longfeng" apple and its large-fruited bud sport variety "Grand Longfeng" most of the differential genes expressed were related to auxin signaling, including the auxin synthetic genes MdTAR1 and MdYUCCA6 (Buetal., 2020). Two of the QTLs were found to be conserved on linkage group (LG) 8 (designated fw2) and LG 15 (designated fw1) across the segregating populations. The major effect genes include auxin response factors and APETELLA 2 family transcription factors as MdARF6 and MdARF106 and MdAP2. In addition, the miRNAs, miR172g, miR172h and mi172p are indicated to be important for fruit enlargement consistent with the role to control fruit size (Duan *et al.*, 2017) [12]. The overexpression of miR172p negatively regulates the fruit size in transgenic

Royal Gala by targeting AP2 TFs and its expression was reduced by introducing a mutant allele of the gene (Yao *et al.*, 2015) [43]. Recently, GWAS analysis revealed 34 QTNs significantly associated with size-related traits and confirmed that the size related traits could be present on all the 17 chromosomes except for chromosome number 10 and 15.

Apple fruit shape

Apple is a variously shaped fruit ranging from conical to spherical and its shape is determined by a set of genetic and epigenetic factors. It is a quantitative trait controlled by several polygenes (Brown, 1960) [4]. Fruit shape index (FSI) which is the ratio of fruit height to width is mainly used to determine shape of the fruit. Some studies have shown that the fruit shape index of apple is a quantitative trait controlled by five pairs of genes (Sun *et al.*, 2012) [31]. Bulk segregant analysis (BSA) on two subsets of 30 seedlings, 30 seedlings with large FSI and 30 seedlings with small FSI resulted in the discovery of four genomic regions located at four linkage groups (10, 11, 12 and 13) at short distance of the SSR markers CH02c11, CH04a12, CH03c02 and GD147 respectively and one AFLP marker, M-CTA/E-AGG-0240 associated with FSI (Sun *et al.*, 2012) [31]. 45 QTLs for apple fruit size, shape, length, and diameter were identified from a 'Jonathan' × 'Golden Delicious' population, of the 19 QTLs for fruit length and diameter, three co-localized with QTLs for fruit shape (Chang *et al.*, 2014) [7]. However, to date, the crucial genes that regulate apple fruit shape have not been identified.

Fruit aroma

Fruit aroma is a complex trait influenced by both genetic and epigenetic factors that regulate the biosynthesis of volatile organic compounds (VOCs). It is a complex interplay of more than 300 volatile substances including esters, aldehydes, alcohols, ethers etc. It involves diverse volatiles multiple synthetic pathways and multiple regulatory genes. In apple, LG2, containing 2 QTLs and LG 15, containing 1 QTL are focal linkage groups for fruit aroma (Zini *et al.*, 2005; Dunemann *et al.*, 2009; Costa *et al.*, 2013) [8, 13, 46]. Except for LG8, LG10, and LG13, QTLs associated with fruit aroma may be localized to the remaining 14 LGs. In apple, for several enzymes crucial for aroma synthesis, genes have been cloned and identified, such as MdLOX1 encoding lipoxygenases (Schiller *et al.*, 2015) [29], MdAAT1 and MdAAT2 encoding alcohol acyltransferases (Li *et al.*, 2006; Dunemann *et al.*, 2012) [14, 23], and MdADH1 and MdADH2 encoding alcohol dehydrogenases (Echeverria *et al.*, 2004). In aldehyde type, there is upregulation of MdFAD, MdADH while down regulation of MdAAT, MdLOX, MdNAC1, MdMYB5, MdERF8 and there is low emission of aroma volatiles. In ester type, MdLOX, MdAAT, MdHPL, MdBCAT, MdPAL, MdNAC1, MdMYB6, MdZIP44 are upregulated and the emission of aroma volatiles is high. However, to evolve genetic mechanism and crucial regulatory genes associated with apple fruit aroma, further study is required. Epigenetic modifications, such as DNA methylation and histone modifications, also contribute to the regulation of fruit aroma.

Organic acids: The critical component determining apple fruit quality is acidity. In apple, a number of organic acids

contribute to the fruit acidity, malic acid being the prominent and constitutes to about 80% of them. Previous studies reported two major acidity quantitative trait loci (QTLs) on linkage groups (LGs) 16 (Ma) and 8 (Ma3), respectively (Ban *et al.*, 2020) [2]. It is controlled by a major gene Ma and minor gene (Verma *et al.*, 2019) [37]. Being dominant in function, homozygous recessive apples (mama) exhibit low acidity while the homozygous dominant and the heterozygous ones exhibit high to moderate acidity (Xu *et al.*, 2012) [42]. Among the 12-19 candidate genes on major Ma locus, one of which encodes an aluminum activated malate transporter, designated MdALMTII (or Ma1) is considered to be the primary gene that determines the Ma locus and fruit acidity, a SNP mutation (A/G) in the coding sequence of Ma1 leads to premature termination of translation and reduces the malic acid content (Bai *et al.*, 2012) [1].

Fruit storage

Apple's fruit storability is a crucial commercial characteristic that directly affects the fruit's shelf life and commodity value. It is a quantitative trait controlled by many genes. Presence of an allele (*MdACS1-2*) of this gene is associated with low internal ethylene concentration in some apple cultivars and hence storability increases and *MdACS1-1/-2* heterozygous and *MdACS1-1/-1* homozygous cultivars show higher ethylene production, the fruit softens readily, and is generally intolerant of storage (Oraguzie *et al.*, 2004) [28]. In apple, *MdPG1*, a key gene belonging to the *polygalacturonase* gene family, was mapped on chromosome 10 and co-localized within the statistical interval of a major hot spot QTL associated to several fruit texture sub-phenotypes (Longhi *et al.*, 2013) [24]. On the QTL hotspot of chromosome 3, an 8-bp deletion in the *MdERF3* promoter disrupted MdDOF5.3 binding, reduced *MdERF3* expression, relieved the inhibition on *MdPGLR3*, *MdPME2*, and *MdACO4* expression, and ultimately decreased flesh firmness and crispness retainability. From a QTL on chromosome 16, a 3-bp deletion in the *MdERF118* promoter decreased its expression by disrupting the binding of MdRAVL1, which increased *MdPGLR3* and *MdACO4* expression and reduced flesh firmness and crispness retainability (Wu *et al.*, 2021) [40]. By GWAS analysis, QTLs associated with fruit firmness have been detected on chromosomes 12, 16, and 17, and three polygalacturonases, one pectinesterase, and one glucan endo-1,3--glucosidase have been identified, associated with cell wall modifications (Duan *et al.*, 2017) [12]. The difference in storage traits between "Fuji" and "Mondial Gala" is attributed to a SNP mutation (T/T in "Fuji" and G/T in "Mondial Gala") in the exon of the Md PG1, which changes the amino acid from valine to phenylalanine (Costa *et al.*, 2010) [9].

Fruit ripening

Apple fruit ripening is a quantitative trait controlled by multiple genes. The NAC family Tfs and the AP2/ERF family TFs are known to have role in apple ripening. Ethylene is an important regulator of fruit ripening, and ethylene biosynthesis, ethylene receptors, and ethylene response related genes all affect fruit ripening (Tan *et al.*, 2013) [33]. In addition to *MdACO1*, MdSnRK2.4 and MdSnRK2.9 interacted with another rate-limiting enzyme, 1-aminocyclopropane-1-carboxylic acid synthase 1

(MdACS1), enhancing its stability by phosphorylating two sites. The higher *MdACO1* expression and enhanced *MdACS1* protein stability increased ETH production, promoting ripening. In apple, SnRK2-1phosphorylated the corresponding sites of MdHB1 and MdHB2 transcription factors to increase their stability and transcriptional activity there by promoting ripening (Jia *et al.*, 2022)^[19]. MdHDT3, a histone deacetylase suppressed the expression of key genes involved in ethylene biosynthesis (*MdACS1* and *MdACO1*) via deacetylation, thereby negatively regulating ethylene biosynthesis. This provides insight into the molecular mechanism by which the histone deacetylase MdHDT3 inhibits ethylene synthesis in apple fruit from an epigenetic perspective (Wang *et al.*, 2025)^[39].

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