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REVIEW ARTICLE

Selective Accumulation of Anthocyanins in Black Chokeberry Fruit and Its Environmental Responses

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ABSTRACT: Ripe black chokeberry (Aronia melanocarpa) fruit is rich in cyanidin glycosides, yet anthocyanin accumulation does not always coincide with changes in other phenolic compounds, sugar metabolism, or fruit growth. This review integrates a reanalysis of published experimental data to examine the physiological and molecular basis of selective anthocyanin accumulation and its responses to environmental conditions. During fruit development, a decline in proanthocyanidin concentration does not necessarily imply a decrease in the amount accumulated per fruit, whereas concurrent declines in anthocyanin concentration and fruit mass during late ripening highlight the importance of pigment retention. Across three cultivars, hexose concentrations increased proportionally much more than sorbitol concentrations during ripening. Reanalysis of data from 23 batches of ripe 'Nero' fruit yielded Pearson correlation coefficients of −0.128, −0.029, and −0.190 between anthocyanin concentration and glucose, fructose, and sorbitol concentrations, respectively, contrasting markedly with the strong positive correlations reported across developmental stages. Germplasm comparisons revealed that fruit with similar total anthocyanin concentrations could differ by more than 20-fold in the ratio of cyanidin galactoside to arabinoside. Sensitivity analysis of tissue composition indicated that anthocyanin concentrations were more responsive to changes in the peel mass fraction than were those of flavonols and hydroxycinnamic acids. However, the reduction in fruit size caused by sustained water deficit was not accompanied by an increase in anthocyanin concentration. Collectively, the available evidence identifies the metabolic utilization of sorbitol, the formation and retention of specific glycosides, and the interplay between tissue-specific metabolism and fruit growth under different environmental conditions as key physiological and molecular questions underlying anthocyanin accumulation in black chokeberry.

Keywords: Black Chokeberry; Anthocyanins; Proanthocyanidins; Sorbitol; Glycosylation; Fruit Development; Environmental Responses

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1. INTRODUCTION

Ripe black chokeberry (Aronia melanocarpa) fruit is rich in anthocyanins and proanthocyanidins, with cyanidin 3-O-galactoside and cyanidin 3-O-arabinoside constituting the major anthocyanin components [1, 2]. This chemical profile emerges through a distinct developmental sequence: young fruit contains high concentrations of proanthocyanidins and phenolic acids, whereas anthocyanins accumulate primarily after the onset of coloration [3–5]. The high anthocyanin content characteristic of ripe fruit reflects differences in the relative accumulation of phenolic compounds during development. Whether this pattern arises from changes in the activity of biosynthetic branches or is associated with fruit growth and metabolite turnover remains to be elucidated.

The relationship between sugar metabolism and anthocyanin accumulation also exhibits noteworthy physiological features during fruit development, sorbitol, glucose, and fructose concentrations are strongly positively correlated with anthocyanin concentration [6]. During the

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mature-fruit harvest period, however, continued sorbitol accumulation can coincide with declining anthocyanin concentration [7]. Fruit grown at different cultivation sites can also exhibit substantial differences in anthocyanin concentration despite similar soluble solids contents [8]. Given the importance of sorbitol in the sugar profile of black chokeberry, its metabolic utilization and relative abundance in relation to hexoses may offer greater mechanistic insight than changes in sugar concentration alone.

Germplasm variation in black chokeberry reveals another feature of anthocyanin formation: fruit with similar total anthocyanin concentrations may have markedly different glycoside profiles [9, 10]. Moreover, both AmMYB10 and AmMYB114 exhibit changes in expression during fruit development but differ in their ability to induce anthocyanin accumulation in heterologous functional assays [11]. These findings shift the research focus from overall activation of the biosynthetic pathway toward functional differences among transcription factors and the formation of specific glycosides. In this review, selective anthocyanin accumulation refers primarily to developmental changes in anthocyanin concentration relative to other phenolic components and differences in the relative accumulation of individual anthocyanin glycosides.

Water, light, and nutrient availability can influence fruit metabolism as well as growth and ripening. Because anthocyanins are highly enriched in the peel [2], differential tissue growth induced by environmental conditions [12] may also alter the phenolic profile measured in whole fruit. By reanalyzing published experimental data, this review focuses on the developmental relationship between proanthocyanidins and anthocyanins, the temporal uncoupling of sugar accumulation and pigment enrichment, the formation of specific glycosides, and the influence of fruit growth on environmentally responsive phenotypes.

Given the complex genetic, ploidy, and taxonomic relationships within the genus Aronia [9, 13], this review also includes related commercially cultivated taxa. The identities assigned to plant materials in the original studies are retained when discussing germplasm comparisons and molecular functions.

Literature selection and data reanalysis. This review combines a question-driven critical literature review with descriptive data reanalysis, prioritizing studies of black chokeberry fruit development, metabolic composition, and environmental treatments that clearly identify plant materials, analytical methods, and quantitative results. Physiological intervention, enzymological, and gene function studies in other fruit crops are used for comparative mechanistic analysis.

The reanalysis primarily comprises conversions between fruit mass and metabolite concentration to estimate metabolite amounts, calculations of sugar andanthocyanin glycoside ratios, correlation analysis between sugar and anthocyanin concentrations, and sensitivity analysis of fruit tissue composition. For correlation analysis, samples were matched by their identifiers in the original studies, with each sample batch treated as an observational unit; Pearson correlation coefficients and Spearman rank correlation coefficients were calculated. Compositional ratios and metabolite amounts were calculated from the means reported in the original studies, retaining their measurement bases and reference-standard equivalents.

For studies lacking complete fruit mass data, threshold analysis was used to assess the potential contribution of growth dilution. For data with an unspecified measurement basis, calculations under alternative assumptions were compared. Technical replicates were not treated as independent biological samples, absolute concentrations obtained using different analytical methods or measurement bases were not pooled, and statistical significance was not reassessed from published means.

2. SDIFFERENTIAL ACCUMULATION OF PHENOLIC COMPOUNDS DURING FRUIT DEVELOPMENT

2.1. The developmental relationship between fruit growth and proanthocyanidin accumulation

Proanthocyanidin and anthocyanin concentrations follow distinct trajectories during black chokeberry fruit development. Gralec et al. [3] found that proanthocyanidin concentration in 'Nero' was high in young fruit, subsequently declined, and rebounded slightly during late ripening, whereas anthocyanins accumulated primarily after the onset of coloration. Dobros et al. [4] similarly reported high concentrations of chlorogenic acid derivatives during early fruit development, followed by a decline accompanied by substantial accumulation of cyanidin glycosides.

As fruit development entails increases in both water and dry matter, a decrease in metabolite concentration may result either from a reduction in the total amount per fruit or from accumulation proceeding more slowly than fruit growth. Even when concentrations are expressed on a dry weight basis, dilution caused by dry matter accumulation remains possible.

Sosnowska et al. [5] analyzed fruit at four developmental stages and found that, from young fruit in May to ripe fruit in August, proanthocyanidin concentration decreased by 86.2%, whereas the fresh mass of 100 berries increased to 10.7 times its initial value (Figure 1A). Such pronounced fruit growth may cause proanthocyanidin concentration and the amount accumulated per fruit to follow different trajectories.

Let M denote the fresh mass per fruit, f the dry matter mass fraction, and C the metabolite concentration on a dry weight basis. The ratio of the measured metabolite amount per fruit (A) between two developmental stages is then given by:

$$A_2/A_1 = (C_2/C_1) \times (M_2/M_1) \times (f_2/f_1) \quad (1)$$

Calculations based on the reported values indicate that, provided the dry matter mass fraction of ripe fruit is at least 67.9% of that of young fruit in May, the estimated measured

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amount of proanthocyanidins per ripe fruit will be no lower than that in young fruit. Thus, although ripe fruit contains a much lower proanthocyanidin concentration, its measured amount per fruit is not necessarily lower than at the beginning of development.

The complete developmental trajectory reveals a more specific issue. From May to June, proanthocyanidin concentration remained nearly unchanged, whereas both fruit fresh mass and dry matter mass fraction increased, indicating that proanthocyanidin accumulation can continue during young fruit growth. From June to July, proanthocyanidin concentration decreased from 6.76 to 0.74 g CYE/100 g DW. If the measured amount per fruit remained unchanged, fruit dry mass would have had to increase to approximately 9.1 times its June value However, estimates based on the fold change in fresh mass reported in the original study and the 32.5% reduction in dry matter mass fraction suggest that dry mass increased only approximately 3.3-fold over this period (Figure 1B). These quantitative relationships suggest a stage-specific reduction in the measured proanthocyanidin amount during the transition from green to semi-ripe purple fruit, rather than growth dilution alone. Identifying this transition period, rather than simply comparing endpoint concentrations in young and ripe fruit, provides a more informative basis for investigating the metabolic fate of proanthocyanidins during rapid fruit growth and coloration.

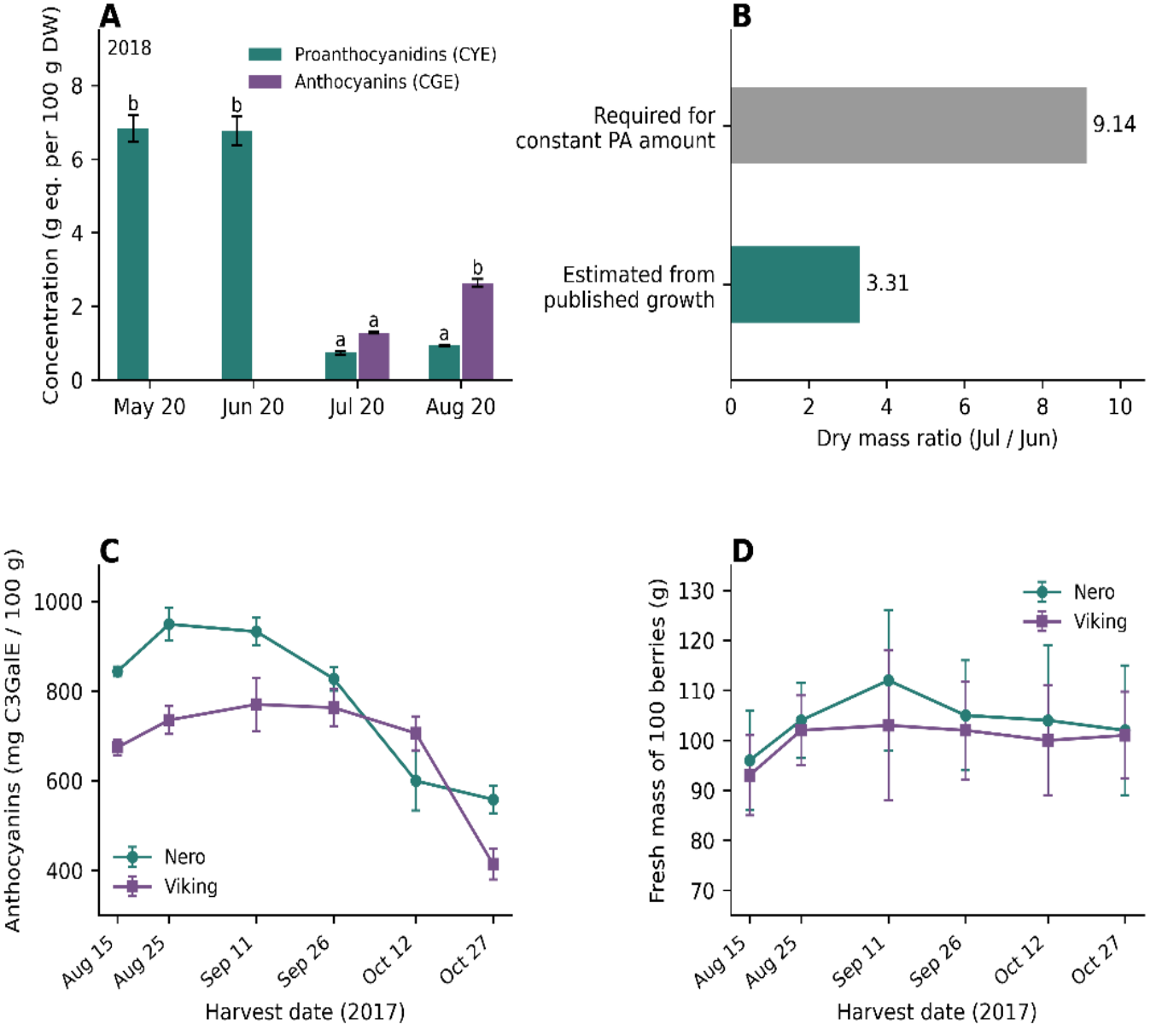


Fig. 1. Differential accumulation of phenolic compounds during black chokeberry fruit development and its relationship with fruit growth.(A) Proanthocyanidin and anthocyanin concentrations on a dry weight basis at different developmental stages; (B) growth-dilution threshold analysis of the decline in proanthocyanidin concentration from June to July; (C) changes in anthocyanin concentration during the mature-fruit harvest period in 'Nero' and 'Viking'; (D) corresponding changes in the fresh mass of 100 berries.

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2.2. Metabolic interpretation of the relationship between proanthocyanidin and anthocyanin accumulation

Proanthocyanidins and anthocyanins share some precursors in flavonoid metabolism. Dihydroflavonols are converted into leucoanthocyanidins by dihydroflavonol 4-reductase (DFR), followed by reactions involving anthocyanidin synthase (ANS), leucoanthocyanidin reductase (LAR), and anthocyanidin reductase (ANR), among others, to form anthocyanidins and flavan-3-ols. Proanthocyanidin formation further involves the assembly and polymerization of starter and extension units [14]. These metabolic connections provide a biochemical basis for substrate competition between biosynthetic branches, but changes in end-product concentrations alone are insufficient to determine actual flux partitioning.

Dobros et al. [4] linked declining chlorogenic acid concentration with anthocyanin accumulation and discussed the possibility that chlorogenic acid might serve as a precursor for anthocyanin formation. However, inverse changes in phenolic acid and anthocyanin concentrations are not sufficient evidence that carbon skeletons from the former are incorporated into the latter. Similarly, the coincidence of declining proanthocyanidin concentration in young fruit with fruit coloration does not establish whether pre-existing proanthocyanidins contribute to subsequent anthocyanin biosynthesis.

Studies of ripening reveal more diverse relationships between these two classes of flavonoid metabolites. Sosnowska et al. [5] found that anthocyanin concentration approximately doubled from July to August, while proanthocyanidin concentration also tended to rebound, although the latter change was not statistically significant. Bolling et al. [7] reported that proanthocyanidin concentration in ‘Viking’ juice increased by 64% over successive harvests, whereas anthocyanin concentration declined after reaching a high value in the fifth week. A multisite study of a related commercially cultivated taxon by King et al. [15] further demonstrated marked interannual variation in proanthocyanidin concentration during the harvest period.

These findings indicate that the relative accumulation of proanthocyanidins and anthocyanins is not governed by a fixed relationship. Anthocyanin enrichment during ripening can coincide with increasing, relatively stable, or declining proanthocyanidin concentrations. Its physiological basis should therefore be interpreted in relation to upstream resource availability, the activity of branch reactions, and product turnover.

Stable isotope tracing studies in grapes provide comparative evidence for understanding pigment loss. Mori et al. [17] found that, at a maximum temperature of 35 °C, anthocyanin content in grape skins fell to less than half that of the control maintained at a maximum of 25 °C, although most anthocyanin biosynthesis-related genes were not transcriptionally repressed to a comparable extent. Reduced retention of previously formed, labeled anthocyanins at 35 °C indicates that high temperature can influence the metabolic fate of pigments after their formation.

Black chokeberry proanthocyanidins exhibit a high degree of polymerization. Research cited by Kaloudi et al. [2] indicates that fractions with a degree of polymerization greater than 10 can account for more than 80% of total procyanidins. Polymerization state, oxidation, and binding to tissue constituents may alter proanthocyanidin extractability, and different analytical methods also respond differently to polymeric structures [3, 5, 15–16]. Consequently, the measured decline in proanthocyanidins during fruit development may reflect changes in both metabolite pools and analytical recovery.

For the stage-specific decline in measured proanthocyanidin amount identified in Section 2.1, a reduced biosynthetic rate can explain only a decrease in newly accumulated material. If the total amount of pre-existing proanthocyanidins actually declines, metabolic losses and changes in polymerization or tissue binding must also be considered. Separate quantification of extractable and poorly extractable proanthocyanidins, together with analysis of their degree of polymerization and measured amounts per fruit, would help characterize the changes undergone by proanthocyanidins present in young fruit during coloration.

2.3. Net anthocyanin accumulation and pigment retention during late ripening

Anthocyanin enrichment in black chokeberry fruit does not continue until the end of the harvest period. In a successive-harvest study of ‘Nero’ and ‘Viking’, Poyraz Engin and Mert [16] found that the reported mean fresh mass of 100 berries peaked on September 11 in both cultivars and subsequently declined or stabilized, whereas anthocyanin concentration decreased markedly during late ripening (Figure 1C and 1D).

From September 11 to October 27, anthocyanin concentration in ‘Nero’ and ‘Viking’ declined by 40.1% and 46.3%, respectively, whereas neither fresh nor dry mass per fruit, calculated from the reported means, increased. When the concentrations were alternatively assumed to be expressed on a fresh or dry weight basis, both conversions indicated a decline in the measured amount of anthocyanins per fruit. Growth dilution caused by continued fruit growth is therefore unlikely to explain the reduction in anthocyanin concentration during late ripening. Over the same period, condensed tannin concentration in ‘Nero’ increased significantly. Although ‘Viking’ exhibited a similar trend, differences in condensed tannin concentration across its entire harvest period were not statistically significant [16]. The divergent changes among phenolic components during late ripening suggest that anthocyanin decline may involve processes specific to pigment formation and retention rather than a concomitant reduction in activity throughout the phenolic metabolic network.

In black chokeberry, the decline in measured pigment amount per fruit during late ripening still requires discrimination among biological degradation, chemical structural changes, and altered extraction recovery. Its high

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anthocyanin content depends not only on the capacity for pigment formation during coloration but also on the duration of that capacity and the extent to which formed pigments are retained. Whether individual cyanidin glycosides differ in turnover rates and whether environmental conditions alter their sustained accumulation are important questions for explaining pigment changes during late ripening.

3. RESULTS AND DISCUSSION

3.1. Changes in the relative abundance of sorbitol and hexoses during fruit development

Sorbitol is a major low-molecular-weight carbohydrate in black chokeberry fruit. Yang et al. [6] found that sorbitol concentrations were higher than those of glucose or fructose at different developmental stages in all three cultivars examined: 'Viking', 'McKenzie', and 'Kingstar K1'. Analysis of 23 batches of ripe 'Nero' fruit by Denev et al. [18] likewise identified sorbitol as the most abundant sugar-related component. However, high sorbitol concentration is not the only distinctive feature of sugar metabolism in this species; its relative abundance in relation to hexoses also changes during fruit development.

Recalculation of the sugar composition data from Yang et al. [6] showed that, as fruit developed from the red-tip stage to the ripe dark-purple stage, sorbitol concentrations increased to 2.51–3.62 times their initial values, whereas the combined concentrations of glucose and fructose increased to 11.57–24.67 times their initial values (Figure 2B). Over the same period, the hexose-to-sorbitol mass ratio increased from 0.157–0.287 to 1.067–1.151 (Figure 2A). Among the three sugar-related components measured, the relative proportion of sorbitol decreased from 77.7–86.5% to 46.5–48.4%. Thus, fruit ripening involves not only an overall increase in sugar concentrations but also differential accumulation of individual components.

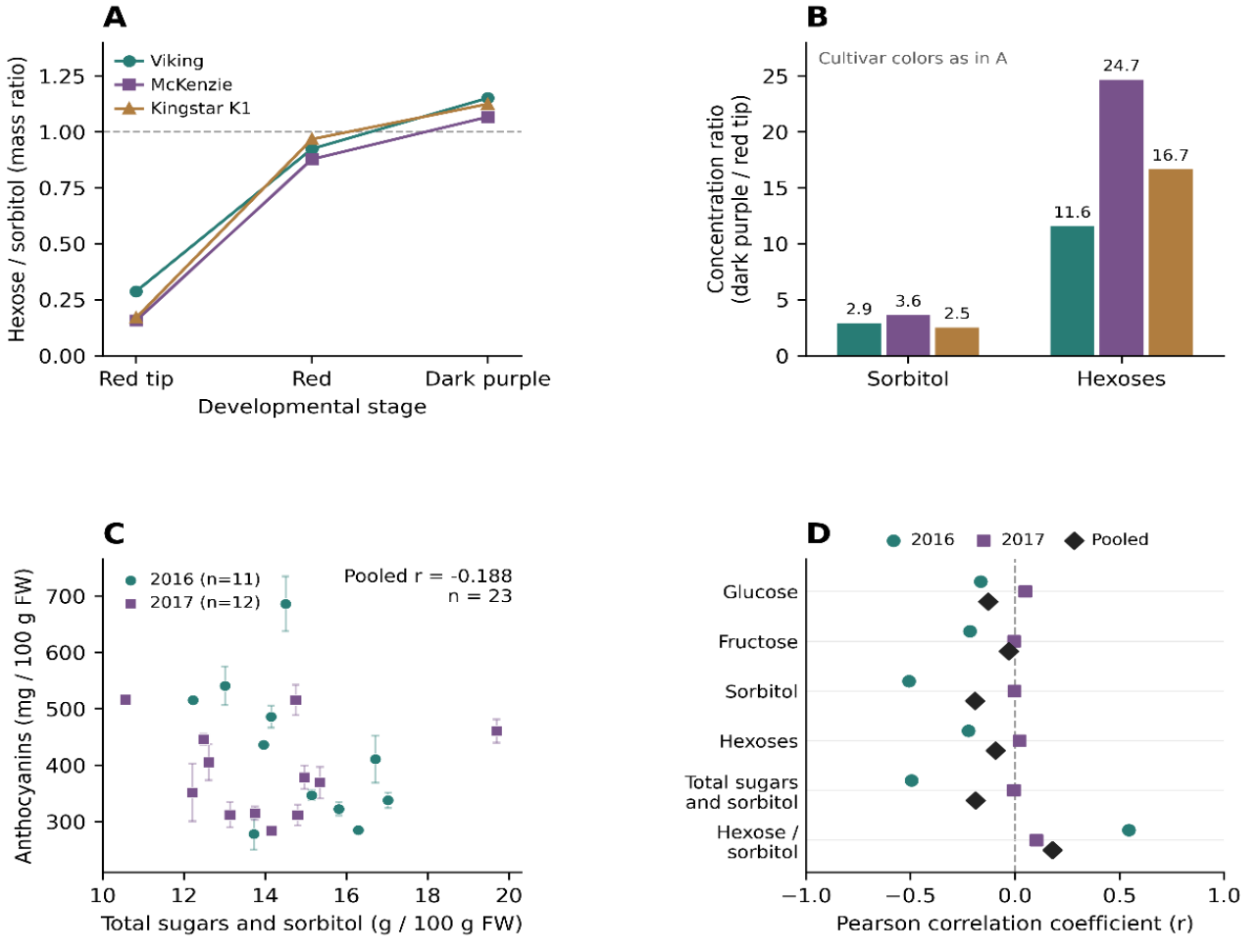


Fig. 2. Developmental changes in sugar composition and their correlations with anthocyanin concentration in black chokeberry fruit. (A) Hexose-to-sorbitol mass ratios at different developmental stages in 'Viking', 'McKenzie', and 'Kingstar K1'; the dashed line denotes equal mass concentrations of the two components. (B) Fold changes in sorbitol and hexose concentrations from the red-tip to the ripe dark-purple stage in the three cultivars. (C) Relationship between total sugar and sugar alcohol concentration and anthocyanin concentration in 23 batches of ripe 'Nero' fruit. (D) Pearson correlation coefficients between sugar metabolism indices and anthocyanin concentration.

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Table 1. Correlations between sugar metabolism indices and anthocyanin concentration in ripe 'Nero' fruit.

Sugar metabolism index	2016 Pearson r (n = 11)	2017 Pearson r (n = 12)	Pooled Pearson r (n = 23)	Pooled Spearman ρ
Glucose	−0.163	0.050	−0.128	−0.234
Fructose	−0.215	−0.003	−0.029	−0.128
Sorbitol	−0.506	−0.001	−0.190	−0.200
Hexose concentration	−0.222	0.022	−0.092	−0.217
Total sugars and sugar alcohol	−0.495	−0.004	−0.188	−0.245
Hexose/sorbitol	0.545	0.103	0.180	0.144

In contrast, sorbitol remained the predominant component in the ripe 'Nero' fruit analyzed by Denev et al. [18], indicating that convergence of hexose and sorbitol concentrations is not a universal feature of black chokeberry ripening. Nevertheless, developmental shifts in sugar composition warrant investigation from the perspective of source–sink carbon metabolism.

Rosaceous fruit trees such as apple and pear use sorbitol and sucrose as long-distance carbon transport forms. After entering sink tissues, sorbitol can be converted into fructose by sorbitol dehydrogenase (SDH) [19, 20]. By suppressing the expression of sorbitol-6-phosphate dehydrogenase in apple leaves, Teo et al. [20] reduced the sorbitol-to-sucrose ratio in leaves and phloem sap by approximately 90% and 75%, respectively. SDH activity in fruit decreased, glucose concentration increased, and fructose, starch, and malic acid concentrations decreased, while fruit mass and firmness remained largely unchanged. This study demonstrates that alterations in the forms of carbon transported from source organs can reshape fruit sugar metabolism without necessarily producing marked changes in fruit growth phenotypes.

The preferential accumulation of hexoses relative to sorbitol during black chokeberry ripening may be associated with sorbitol conversion, sucrose hydrolysis, and the storage of individual sugar components. High sorbitol concentration in fruit may reflect greater carbon import or be related to the capacity for sorbitol conversion in sink tissues. Sorbitol transport, accumulation, and utilization should therefore be investigated as distinct physiological processes.

3.2. The developmental context of sugar–anthocyanin correlations

Sugar enrichment and anthocyanin accumulation exhibit substantial temporal concordance during fruit development. Yang et al. [6] reported Pearson correlation coefficients of 0.920, 0.911, and 0.907 between total anthocyanin concentration and glucose, fructose, and sorbitol concentrations, respectively. However, because both sugar and anthocyanin concentrations increase during ripening, these correlations may reflect contributions from both sugar-mediated metabolic regulation and shared developmental progression.

To examine sugar–anthocyanin relationships within ripe fruit, this review reanalyzed data published by Denev et al. [18] for 23 batches of ripe 'Nero' fruit. Sugar composition and anthocyanin concentration data were matched individually using the sample identifiers in Tables 1 and Figure 3 of the original study, and correlation coefficients were calculated separately for each year and for the pooled samples (Table 1).

In ripe 'Nero' fruit, Pearson correlation coefficients between anthocyanin concentration and glucose, fructose, and sorbitol concentrations were −0.128, −0.029, and −0.190, respectively, contrasting markedly with the strong positive correlations reported across developmental stages. Pearson and Spearman correlation coefficients between total sugar and sugar alcohol concentration and anthocyanin concentration were −0.188 and −0.245, respectively. The overall correlation between the hexose-to-sorbitol ratio and anthocyanin concentration was also weak (Figure 2C and 2D).

In particular, ripe fruit batches 2016_5 and 2016_7 contained total sugar and sugar alcohol concentrations of 13.72 and 14.50 g/100 g FW, respectively, differing by only approximately 5.7%. Their anthocyanin concentrations, however, were 278.2 and 686.0 mg/100 g FW, respectively, with the latter approximately 2.47 times the former [18]. Similar sugar concentrations can therefore be associated with substantially different anthocyanin concentrations.

The two studies differed in cultivar, cultivation environment, and sampling design, and restricting analysis to the ripe stage may also narrow the range of the variables. Differences in correlation coefficients therefore do not directly establish a developmental-stage-dependent modulation of sugar responsiveness. Nevertheless, the successive-harvest study by Bolling et al. [7] further showed that glucose and fructose concentrations in 'Viking' juice stabilized around the fourth week, anthocyanin concentration declined after reaching a high value in the fifth week, and

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sorbitol concentration increased by approximately 40% throughout the harvest period. Sugar accumulation and anthocyanin enrichment thus follow distinct temporal trajectories during late ripening.

Collectively, these results indicate that strong positive sugar–anthocyanin correlations across developmental stages are insufficient to explain differences in pigment concentration among ripe fruit. Sugar availability, metabolic utilization of sugars, and the functional state of the coloration program should be investigated as distinct physiological factors influencing anthocyanin formation. Moreover, soluble solids content (SSC) is an aggregate index derived from refractive measurements and is not equivalent to the actual concentrations of individual sugars in fruit. Assessing fruit carbon metabolism solely on the basis of SSC is unlikely to reveal how specific sugars relate to anthocyanin formation.

3.3. Metabolic utilization of sugars and regulation of fruit coloration

The effects of sugars on anthocyanin formation involve both the supply of carbon skeletons, energy, and glycosyl donors and sugar-sensing-mediated transcriptional regulation. Individual sugars differ in their metabolic properties and signaling effects; changes in sugar composition may therefore elicit physiological responses distinct from those resulting from changes in total sugar concentration.

Using an in vitro culture system for intact detached grape berries, Dai et al. [21] found that glucose, fructose, and sucrose all promoted anthocyanin accumulation, with glucose and fructose exerting stronger effects. Despite enhanced anthocyanin accumulation under sugar supplementation, the concentration of the biosynthetic precursor phenylalanine decreased, accompanied by changes in the expression of related genes, including UFGT. These results indicate that sugar-promoted anthocyanin formation does not necessarily involve an increase in precursor concentration but may instead involve changes in substrate utilization and downstream metabolic capacity.

Studies of sugar sensing in apple further reveal the connection between sugar signaling and transcription factor function. Hu et al. [22] found that the hexokinase MdHXK1 responds to glucose signaling by phosphorylating MdbHLH3 at Ser361, thereby enhancing its protein stability and transcriptional activation capacity. Liu et al. [23] found that MdSnRK1.1 promotes the degradation of MdJAZ18 through phosphorylation, relieving its repression of MdbHLH3 and thereby promoting anthocyanin and proanthocyanidin biosynthesis. Both sugar-responsive pathways involve changes in the function of bHLH regulatory proteins, indicating that the metabolic effects of sugars depend not only on their concentrations but also on the state of downstream regulatory networks.

In black chokeberry, coexpression of AmMYB10 and AmbHLH33 enhances anthocyanin accumulation in a heterologous system [11]. However, functional evidence for direct regulation of AmbHLH33 by sugar-sensing systems is currently lacking. In light of the developmental changes in the relative abundance of sorbitol and hexoses, a specific mechanistic question emerges: does metabolic conversion of sorbitol contribute to the establishment of fruit coloration capacity by altering hexose availability or sugar-sensing status?

Meanwhile, the continued accumulation of sugars despite declining anthocyanin concentration during late ripening suggests that the maintenance of coloration capacity and the retention of pre-existing pigments may be constrained by other processes. Whole-fruit sugar concentrations also do not directly reflect the carbon resources and nucleotide sugars available within peel cells. Independent sugar-supply interventions at different developmental stages, combined with measurements of sorbitol conversion, regulatory protein function, and anthocyanin formation and loss, are therefore needed to establish the actual roles of carbon resources and sugar signaling at different stages of fruit coloration.

4. MOLECULAR BASIS OF SELECTIVE ANTHOCYANIN ACCUMULATION

4.1. Germplasm variation in anthocyanin concentration and glycoside composition

The major anthocyanins in black chokeberry include cyanidin 3-O-galactoside, cyanidin 3-O-arabinoside, cyanidin 3-O-glucoside, and cyanidin 3-O-xyloside, with the first two accounting for the vast majority [1, 9]. These compounds share the same aglycone but differ in their glycosyl moieties. Variation in anthocyanin concentrations and glycoside proportions among accessions provides a basis for investigating the relationship between overall pigment formation capacity and the accumulation of specific products.

In a study of five Aronia cultivars, Gerasimov et al. [1] reported total anthocyanin concentrations of 388.1–620.5 mg C3GlE/100 g FW, with the highest value approximately 1.60 times the lowest. By contrast, the ratio of cyanidin galactoside to arabinoside varied only between 2.44 and 2.86 (Figure 3A and 3B). Thus, despite substantial variation in anthocyanin concentration among these cultivars, the relative composition of the major glycosides remained comparatively stable.

Wild germplasm exhibits more extensive variation in glycoside composition. Brand et al. [9] found that some diploid black chokeberry accessions contained a high proportion of cyanidin galactoside and a low proportion of arabinoside. In a study of related accessions, Connolly [10] reported that, at the first harvest in 2010, total anthocyanin concentrations in UC009 and UC023 were 60.7 and 63.1 μmol C3GlE/g DW, respectively, whereas their galactoside-to-arabinoside ratios were 53.55 and 2.36, differing by approximately 22.7-fold. At the second harvest, the difference between the corresponding ratios reached 30.5-fold (Figure 3C and 3D).

In a subsequent study of fruit development, Mahoney et

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al. [11] similarly observed a high proportion of cyanidin galactoside and a low proportion of arabinoside in UC009. This distinctive glycoside composition was not confined to a single harvest, suggesting that it may be associated with the genetic background of the accession.

Despite its very low arabinoside concentration, UC009 accumulated substantial amounts of galactoside without a corresponding reduction in total anthocyanin concentration. This demonstrates that total anthocyanin concentration and specific glycoside composition may exhibit distinct patterns of germplasm variation. Screening accessions solely on the basis of total anthocyanin concentration may overlook metabolic diversity associated with late-stage glycosylation and product retention. The contrasting compositions of UC009 and UC023 also make them candidate materials for investigating cyanidin galactosylation and arabinosylation.

4.2. Differences in the expression and function of MYB regulators

Mahoney et al. [11] conducted peel transcriptome analyses at four developmental stages in six diploid black chokeberry accessions and found that expression levels of AmPAL2, Am4CL, AmANS, and AmGST were significantly positively correlated with the concentrations of individual cyanidin glycosides. By contrast, AmF3H expression increased during early development and subsequently stabilized, showing no significant correlation with the concentrations of individual cyanidin glycosides. UFGT was not identified as a differentially expressed gene. Anthocyanin accumulation during ripening is therefore accompanied by transcriptional activation of selected metabolic steps rather than coordinated upregulation of all biosynthesis-related genes.

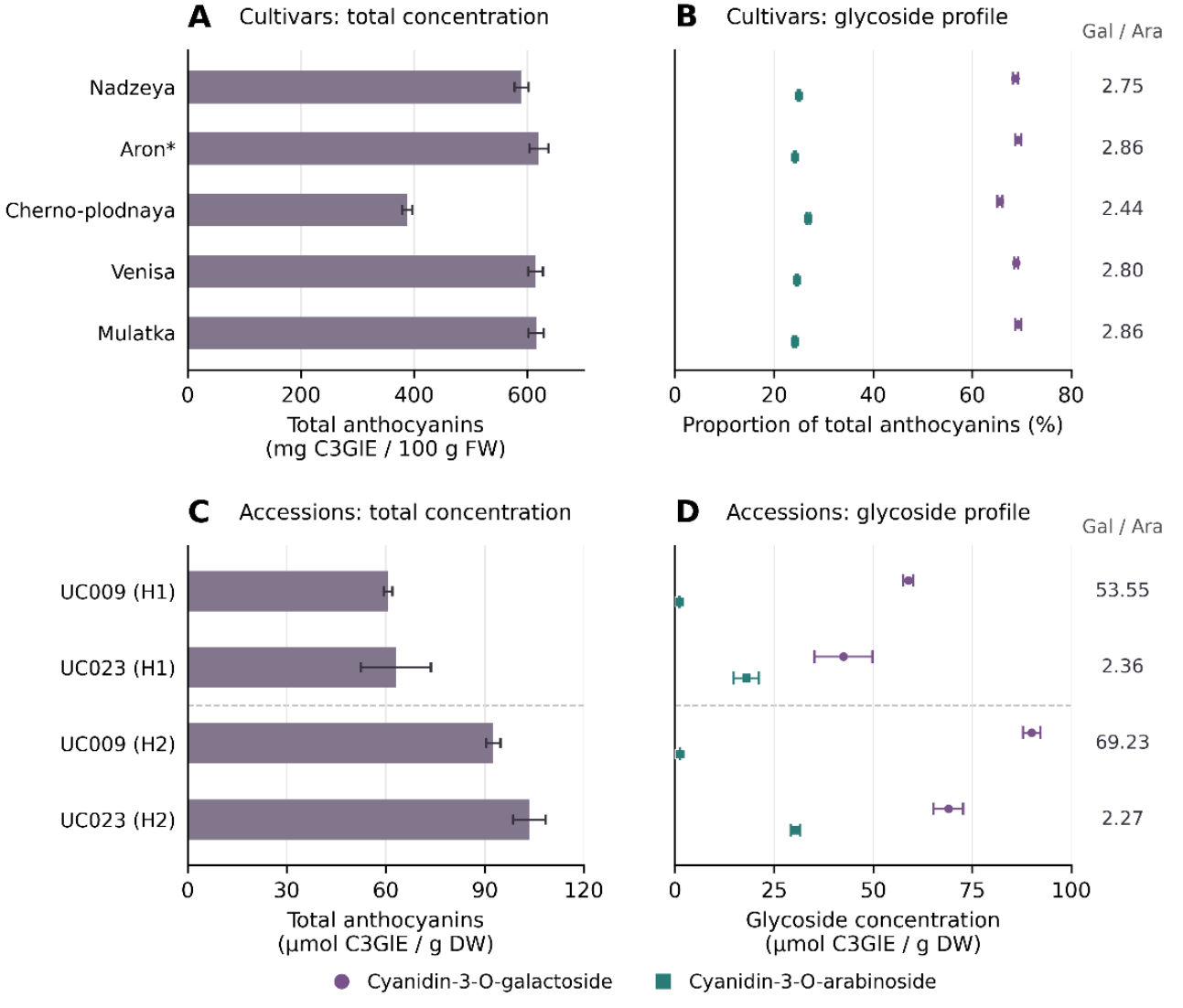


Fig. 3. Germplasm variation in total anthocyanin concentration and major glycoside composition in Aronia fruit.(A) Total anthocyanin concentrations in five Aronia cultivars; (B) proportions of cyanidin 3-O-galactoside and cyanidin 3-O-arabinoside in total anthocyanins and their ratios in the corresponding cultivars; (C) total anthocyanin concentrations in diploid black chokeberry accessions UC009 and UC023 at two harvests in 2010; (D) concentrations of cyanidin 3-O-galactoside and cyanidin 3-O-arabinoside and their ratios in the corresponding accessions.

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Studies of transcription factors reveal even more pronounced discrepancies between expression and function. AmMYB114 was significantly upregulated during fruit development, whereas the increase in AmMYB10 expression was relatively modest. In transient expression assays in Nicotiana benthamiana leaves, however, AmMYB10 induced weak coloration that was enhanced by co-expression with AmbHLH33. Neither expression of AmMYB114 alone nor its co-expression with AmbHLH33 induced detectable anthocyanin accumulation, and co-expression with AmMYB10 did not enhance the activity of the latter [11].

These results differ from the functional behavior of MYB114 in pear. Yao et al. [24] found that pear PyMYB114 activated transcription from the PyDFR and PyUFGT promoters more strongly than PyMYB10, whereas PyMYB10 exerted stronger activation of the PyANS promoter. Co-expression of both factors enhanced the transcriptional activity of the relevant promoters. MYB factors involved in fruit coloration can therefore influence anthocyanin formation through differences in target gene selection and regulatory partners.

The discrepancy between the developmental expression and heterologous activity of black chokeberry AmMYB114 may involve its ability to recognize target promoters or select regulatory partners. Current studies have not identified its direct target genes in black chokeberry, and the possibility that the heterologous system lacks appropriate regulatory conditions cannot be excluded. The actual biological function of AmMYB114 therefore remains to be elucidated in native tissues.

Alternative splicing of AmMYB114 further increases its potential functional diversity. The short splice variant AmMYB114s identified by Mahoney et al. [11] is 104 bp shorter than the full-length transcript and exhibits a shift in the reading frame. Its predicted protein retains the MYB DNA-binding domain but lacks the predicted transcriptional activation domain. In the co-expression assays performed to date, AmMYB114s did not noticeably inhibit the activation activity of AmMYB10. Investigation of this splice variant should therefore not be restricted a priori to a putative anthocyanin biosynthesis-repressing function, but should instead consider its actual DNA-binding capacity and regulatory targets.

Current heterologous functional evidence supports a role for AmMYB10 in promoting anthocyanin formation, and its co-expression with AmbHLH33 suggests potential functional synergy. In contrast, AmMYB114 and its splice variant may participate in distinct developmental or metabolic regulatory processes. Identifying the endogenous target genes of these MYB factors and their effects on different flavonoid products offers greater mechanistic insight than screening anthocyanin regulators solely on the basis of developmental expression levels.

4.3. Formation and retention of specific glycosides

The major anthocyanins in black chokeberry share cyanidin as their aglycone, suggesting that differences in glycoside composition may arise during late-stage reactions in anthocyanin biosynthesis. The types of nucleotide-sugar donors, catalytic selectivity of glycosyltransferases, and extent of retention of individual glycosides after their formation may all influence the final pigment composition.

Clayton-Cuch et al. [25] identified the apple glycosyltransferase MdUGT78T2, which exhibits selectivity for a galactosyl donor. This enzyme catalyzes the formation of the corresponding 3-O-galactosides from both cyanidin and quercetin, with an in vitro catalytic efficiency toward quercetin approximately 500 times that toward cyanidin. The ability of a single glycosyltransferase to act on acceptor substrates from different branches of flavonoid metabolism indicates that metabolic connections between flavonols and anthocyanins may extend beyond upstream precursor supply to shared late-stage modification reactions.

The differences in anthocyanin composition between UC009 and UC023 [10] may be associated with differences in galactosylation and arabinosylation capacities, but may also be influenced by nucleotide-sugar availability and glycoside turnover. Addressing this issue requires integrating the acceptor and donor selectivity of candidate glycosyltransferases with tissue nucleotide-sugar composition and the actual glycoside products. Changes in free sugar composition discussed in Section 3 provide a physiological context for investigating nucleotide-sugar metabolism but cannot yet directly explain the relative formation of individual anthocyanin glycosides.

The selective responses of certain quercetin glycosides to field shading [26] further warrant investigation of shared modification enzymes. Considering the dual-acceptor catalytic properties of apple MdUGT78T2, whether black chokeberry possesses a galactosyltransferase capable of acting on both cyanidin and quercetin represents a specific mechanistic question linking variation in anthocyanin composition to the environmental responses of flavonols.

Notably, Mahoney et al. [11] did not identify UFGT as differentially expressed in developing fruit, whereas Hou et al. [27] observed UFGT upregulation in light-induced callus. Because the two studies differed in tissue material and transcriptomic design, it remains unclear whether their annotated UFGT sequences represent the same functional member. Research on these genes should progress beyond general functional annotations toward enzymatic characterization of their specific glycosyl donors and acceptor substrates.

After anthocyanin glycosides are formed, intracellular trafficking and vacuolar storage further influence their accumulation. AmGST expression is markedly upregulated during black chokeberry fruit development and positively correlated with anthocyanin concentration [11]. In apple, Jiang et al. [28] demonstrated through gene functional assays that MdGSTF6 participates in anthocyanin accumulation and that MdMYB1 directly activates its transcription. Hu et al. [29] further showed that MdMYB1 regulates the expression of vacuolar proton pumps and related transporters, affecting vacuolar acidification and anthocyanin accumulation.

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Together, these studies indicate that MYB factors can participate in both pigment biosynthesis and intracellular storage, providing comparative evidence for investigating the potential functional relationship between AmMYB10 and AmGST.

The harvest-period data discussed in Section 2 indicate that pigment loss during late ripening in black chokeberry cannot readily be explained entirely by growth dilution. In light of isotope-tracing evidence for high-temperature-induced loss of pre-existing anthocyanins in grape berries [17], whether the retention of individual cyanidin glycosides changes with fruit ripening and environmental conditions also warrants further investigation. Even if individual glycosides are formed at similar rates, differences in their loss rates may result in markedly different anthocyanin profiles. Selective accumulation of specific anthocyanin glycosides in black chokeberry therefore needs to be examined in terms of both formation and retention. The catalytic properties of glycosyltransferases determine the potential for specific glycoside formation, whereas intracellular trafficking, the vacuolar environment, and product turnover may further modify their actual accumulation. Characterizing variation in these processes among accessions will help explain the distinctive cyanidin glycoside composition of this species and its responses to environmental conditions.

5. RELATIONSHIPS BETWEEN FRUIT GROWTH AND ANTHOCYANIN ACCUMULATION UNDER DIFFERENT ENVIRONMENTAL CONDITIONS

5.1. Tissue distribution of phenolic compounds and differential fruit growth

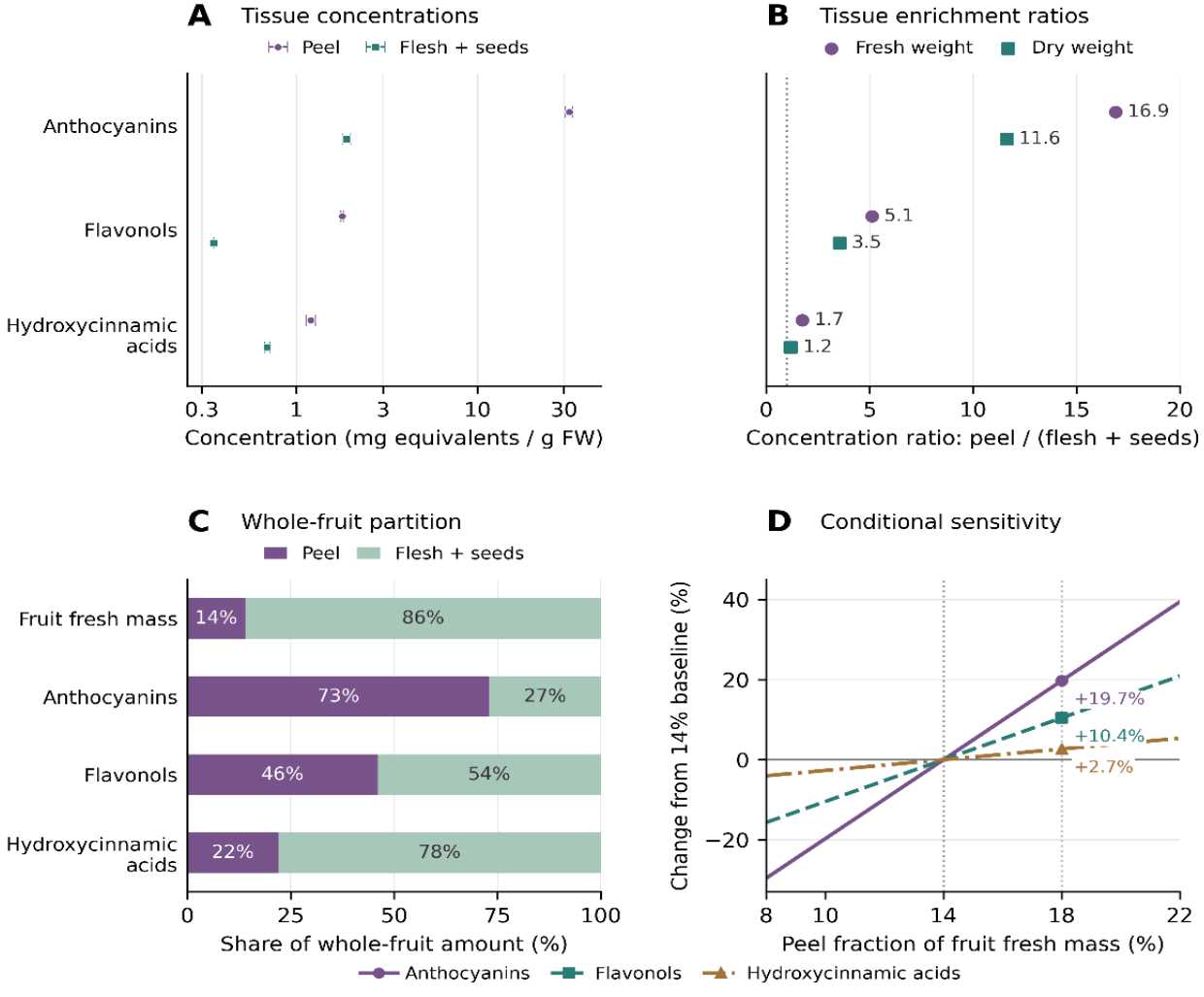


Fig. 4. Tissue distribution of phenolic compounds in black chokeberry fruit and sensitivity of whole-fruit concentrations to changes in the peel mass fraction.(A) Concentrations of anthocyanins, flavonols, and hydroxycinnamic acids in the peel and the combined flesh and seed fraction, with the horizontal axis on a logarithmic scale; (B) peel-to-remaining-tissue concentration ratios for each phenolic class on fresh and dry weight bases; (C) partitioning of fruit fresh mass and the amounts of each phenolic class between the peel and the remaining tissues; (D) sensitivity of whole-fruit phenolic concentrations to changes in the peel fresh mass fraction, assuming constant tissue-specific metabolite concentrations.

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Different classes of phenolic compounds exhibit markedly different distributions within black chokeberry fruit. Kaloudi et al. [2] found that the peel accounted for only 14% of whole-fruit fresh mass but contained approximately 73% of the anthocyanins, 46% of the flavonols, and 22% of the hydroxycinnamic acids. On a fresh weight basis, the anthocyanin concentration in the peel was approximately 16.9 times that in the combined flesh and seed fraction, whereas the corresponding ratios for flavonols and hydroxycinnamic acids were 5.1 and 1.7, respectively. Even on a dry weight basis, anthocyanin concentration in the peel was 11.6 times that in the remaining tissues, indicating that tissue-specific anthocyanin enrichment cannot be attributed solely to differences in water content (Figure 4A–C).

Let f denote the fraction of whole-fruit fresh mass accounted for by the peel, and C_p and C_m denote the metabolite concentrations in the peel and the remaining tissues, respectively. Whole-fruit concentration C can then be expressed as:

$$C = fC_p + (1 - f)C_m \quad (2)$$

Assuming that metabolite concentrations within individual tissues remain constant, the effect of changes in the peel mass fraction on whole-fruit concentration depends on the concentration difference between the two tissue fractions. Sensitivity analysis using the tissue concentrations reported by Kaloudi et al. [2] and a baseline peel fresh mass fraction of 14% showed that, for each one-percentage-point increase in the peel fraction, whole-fruit concentrations of anthocyanins, flavonols, and hydroxycinnamic acids increased by approximately 4.93%, 2.61%, and 0.67% relative to baseline, respectively. When the peel fraction increased from 14% to 18%, the whole-fruit concentrations of the three phenolic classes increased by approximately 19.7%, 10.4%, and 2.7%, respectively (Figure 4D).

This analysis indicates that the same change in tissue composition can elicit phenolic concentration responses of different magnitudes, with anthocyanins being more sensitive to changes in the peel mass fraction. However, because all three phenolic classes measured are more concentrated in the peel than in the remaining tissues, changing the peel fraction alone can only shift their whole-fruit concentrations in the same direction. If different phenolic components respond in opposite directions under ·

5.3. Nutrient supply, crop load, and anthocyanin production capacity

Pigment production capacity in black chokeberry depends on both fruit anthocyanin concentration and yield per plant, and these two attributes do not always respond similarly to cultivation conditions. In a three-year fertilization study of 'Viking', Jeppsson [34] found that increasing the supply of combined nitrogen, phosphorus, and potassium fertilizer promoted vegetative growth and fruit yield, but generally reduced anthocyanin concentration in the juice. Mean yields per plant at the lowest and highest fertilizer rates were 880 and 1,910 g, respectively, while juice anthocyanin concentrations were 1,330 and 880 mg/L, respectively. Differences in both yield and pigment concentration between these treatments were statistically significant. Notably, mean individual fruit mass, soluble solids content, and anthocyanin composition did not differ significantly among fertilizer treatments [34]. The lower anthocyanin concentration at higher fertilizer rates therefore cannot be attributed simply to individual fruit enlargement. Enhanced vegetative growth and increased fruit number may alter carbon demand and assimilate partitioning among organs. However, a significant negative correlation between yield per plant and anthocyanin concentration occurred in only one experimental year, indicating that there is no consistent negative relationship between growth and pigment accumulation.

In a study of the commercially cultivated taxon A. mitschurinii, Green et al. [35] similarly found that higher nitrogen rates generally favored yield formation. However, in 2018 and 2019, juice anthocyanin concentration in the Plot B experiment was higher under an annual nitrogen application rate of 3 g per plant than under 14 g per plant. Together, these studies indicate that fruit yield and anthocyanin accumulation respond differently to nutrient availability and that their resource allocation relationship cannot be inferred solely from fertilizer application rates.

Surveys across cultivation sites also reveal discrepancies between concentration and yield. Won et al. [8] reported fruit anthocyanin concentrations of 949.7 and 440.5 mg/kg in Danyang and Yeongdong, respectively, while fruit yields per plant were 1.6 and 5.8 kg, respectively. Yeongdong thus had a higher fruit yield per plant but a lower fruit anthocyanin concentration. Because cultivation sites differed simultaneously in environmental conditions and management practices, these observational findings cannot independently establish the regulatory effect of crop load on anthocyanin formation. They nevertheless illustrate the limitations of using fruit concentration alone to assess pigment production capacity under cultivation conditions.

Growth and secondary metabolism can also respond positively in concert. Giannakoula et al. [36] found that treatment with a specific combination of biostimulants simultaneously improved photosynthetic physiological parameters in black chokeberry leaves and increased fruit anthocyanin concentration. Although this treatment involves multiple physiological regulatory processes, including mineral nutrition, its results, together with those of fertilization studies, suggest that the effects of improved plant physiological status on secondary metabolism may depend on specific resource availability and metabolic demands, rather than enhanced growth necessarily suppressing pigment accumulation.

For production assessment, whole-fruit anthocyanin output should be calculated from the fruit mass and corresponding mass-based concentration of each harvest batch. If anthocyanins are measured as a volume-based concentration in juice, actual juice volume should be used to evaluate pigment output. Pigment loss and other quality

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changes during late ripening also influence the optimal harvest time. Jeppsson and Johansson [37] found that harvesting one week earlier reduced the browning index by 32% but also decreased anthocyanin content by 20%.

Increasing fruit anthocyanin concentration and improving plant pigment production capacity should therefore be treated as distinct cultivation objectives, with separate consideration of local fruit metabolism, crop load, yield formation, and pigment retention during the harvest period. Appropriate environmental management should be determined according to the intended use of the fruit and actual pigment output.

6. CONCLUSIONS AND KEY SCIENTIFIC QUESTIONS

Anthocyanin accumulation in black chokeberry fruit is accompanied by stage-specific changes in phenolic composition, but changes in the concentrations of individual phenolic compounds do not adequately reflect their actual accumulated amounts or metabolic fluxes. Fruit growth can account for part of the decline in proanthocyanidin concentration, while changes during the transition from green to semiripe purple fruit may also involve metabolic losses of proanthocyanidins or alterations in their tissue-binding state. Concurrent declines in anthocyanin concentration and fruit mass during late ripening further suggest that pigment retention, as well as biosynthesis, warrants attention in explaining anthocyanin accumulation in ripe fruit.

Fruit ripening is accompanied not only by increasing sugar concentrations but also by shifts in the relative abundance of sorbitol and hexoses. Differences in sugar–anthocyanin correlations between studies spanning developmental stages and those restricted to ripe fruit indicate that whole-fruit sugar concentration alone is insufficient to explain pigment variation among ripe fruit. Distinct patterns of variation in total anthocyanin concentration and glycoside composition among accessions, together with differences in the heterologous functions of AmMYB10 and AmMYB114, further direct research toward the metabolic utilization of sugars, target gene selection by transcription factors, and the formation and retention of specific glycosides.

The strong enrichment of anthocyanins in the peel makes their whole-fruit concentration relatively sensitive to changes in tissue mass fractions. Tissue composition effects can explain differences in the magnitude of concentration responses among phenolic classes, but cannot account for responses in opposite directions when tissue-specific concentrations remain constant. Studies of environmental regulation should distinguish changes in local tissue metabolism from compositional effects arising from fruit growth and incorporate pigment accumulation per fruit and yield per plant into their assessments.

Future research should prioritize elucidating the metabolic fate of highly polymerized proanthocyanidins present in young fruit during coloration, testing the roles of sorbitol conversion and sugar sensing in anthocyanin formation, and identifying the enzymes responsible for the formation of the major cyanidin glycosides as well as characterizing their turnover. These questions are directly relevant to the formation of the distinctive phenolic composition of black chokeberry and its responses to environmental variation.

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Ethical Approval

We affirm that this manuscript is an original work, has not been previously published, and is not currently under consideration for publication in any other journal or conference proceedings. All authors have reviewed and approved the manuscript, and the order of authorship has been mutually agreed upon.

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The authors declare that they have no financial or personal interests that could have influenced the research and findings presented in this paper. The authors alone are responsible for the content and writing of this article.

Authors' contributions

All authors contributed equally to this work,

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