

Cultivar-specific regulation of vitamin C metabolism in kiwifruit during postharvest ripening

Xia Liming

Guangxi Institute of Botany, Chinese Academy of Sciences

Ye Kaiyu

Guangxi Institute of Botany, Chinese Academy of Sciences

Liu Cuixia

Guangxi Institute of Botany, Chinese Academy of Sciences

Gao Jianyou

Guangxi Institute of Botany, Chinese Academy of Sciences

Zhu Rongxiang

Guangxi Institute of Botany, Chinese Academy of Sciences

Lin Wei

Subtropical Agriculture Research Institute, Fujian Academy of Agricultural Sciences

Jiang Qiaosheng

Guangxi Institute of Botany, Chinese Academy of Sciences

Wang Faming

36326266@qq.com

Guangxi Institute of Botany, Chinese Academy of Sciences

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Abstract

Vitamin C, mainly in the form of ascorbic acid (AsA), is an important nutritional quality trait in kiwifruit, but its retention during postharvest ripening varies among cultivars. This study aimed to clarify the physiological basis of cultivar-specific AsA stability in kiwifruit during shelf ripening. Three cultivars, 'Hongyang', 'Guihong', and 'Guihai No.4', were stored at $20 \pm 1^\circ\text{C}$ and 85–90% relative humidity for 8 days. Fruit firmness, soluble solids, titratable acidity, ethylene production, respiration rate, AsA content, and the activities of key enzymes involved in AsA biosynthesis and recycling were measured. The results showed that 'Hongyang' had the highest initial AsA content but lost approximately 40% by day 6, accompanied by rapid decreases in GDP-L-galactose phosphorylase and L-galactono-1,4-lactone dehydrogenase activities. In contrast, 'Guihai No.4' softened more slowly, showed lower ethylene and respiration peaks, and maintained relatively stable AsA levels during early ripening, which was associated with higher ascorbate peroxidase and monodehydroascorbate reductase activities. 'Guihong' maintained the lowest AsA level throughout ripening. These findings indicate that postharvest AsA retention in kiwifruit depends on the coordination between biosynthetic capacity and AsA recycling efficiency rather than initial AsA content alone.

1. Introduction

Kiwifruit (*Actinidia* spp.) is valued worldwide for its high vitamin C (ascorbic acid, AsA) content, dietary fiber, and antioxidant properties (He et al., 2025). Compared with citrus and apple, kiwifruit typically contains 2–10 times more AsA per unit fresh weight (Choi et al., 2018; Nishiyama et al., 2004). As an essential water-soluble antioxidant, AsA plays critical roles in scavenging reactive oxygen species, enhancing immune function, and promoting collagen synthesis (Carr & Maggini, 2017). Consequently, maintaining high and stable AsA content during postharvest handling is of significant nutritional and economic importance.

In plants, AsA is mainly synthesized via the L-galactose pathway, where GDP-L-galactose phosphorylase (GGP) acts as the key rate-limiting enzyme (Wheeler et al., 1998; Pant et al., 2009). Recent evidence shows that GGP expression is directly activated by transcription factors such as Cycling Dof Factor 3, promoting AsA accumulation in fruits (Huang et al., 2025). In kiwifruit, GGP activity positively correlates with AsA content (Li et al., 2010). The terminal step is catalyzed by L-galactono-1,4-lactone dehydrogenase (GalLDH), which resides in the mitochondrial inner membrane and links AsA biosynthesis to respiratory metabolism (Leferink et al., 2008; Bartoli et al., 2000). Beyond biosynthesis, AsA homeostasis depends on the ascorbate-glutathione (AsA-GSH) cycle, where ascorbate peroxidase (APX) uses AsA to detoxify H_2O_2 , and monodehydroascorbate reductase (MDHAR), dehydroascorbate reductase (DHAR) and glutathione reductase (GR) regenerate AsA from its oxidized forms (Noctor & Foyer, 1998; Asada, 2006; Foyer & Noctor, 2011). The efficiency of this recycling system directly influences AsA retention during fruit ripening and storage (Chauhan et al., 2022; Vithana et al., 2025). In kiwifruit, cold storage enhances MDHAR and GR activity, delaying AsA degradation (Chen et al., 2020).

Despite these advances, most studies have focused on commercially dominant cultivars such as ‘Hayward’ and ‘Jinyan’, while locally bred or regionally specific varieties remain underexplored (Crowhurst et al., 2008; Han et al., 2016; Viršilė et al., 2019). Moreover, research has emphasized AsA dynamics during fruit development, with limited systematic insight into postharvest ripening and storage (Lee et al., 2019). Postharvest treatments (e.g., cold storage, controlled atmosphere, 1-MCP) show cultivar-dependent effects on AsA retention (Fiutak et al., 2020; Jung et al., 2025), indicating a need for genotype-specific understanding.

Although AsA biosynthesis pathways in kiwifruit have been well characterized, most studies focus on accumulation during fruit development rather than its stability during postharvest ripening. Importantly, postharvest vitamin C loss is not solely driven by degradation but is jointly regulated by biosynthetic suppression and recycling inefficiency. However, the integrated regulation between ethylene signaling, AsA biosynthesis (GGP and GalLDH), and the AsA–GSH recycling system remains poorly understood across different cultivars.

Here, we selected three kiwifruit cultivars of *Actinidia chinensis* with distinct ripening behaviors: ‘Hongyang’ ‘Guihong’, and ‘Guihai No.4’, which are preserved at the Guangxi Institute of Botany. The objectives were to (1) compare their postharvest softening, ethylene production and respiration patterns; (2) determine dynamic changes in AsA content during shelf ripening; (3) analyze key enzyme activities in AsA biosynthesis and recycling; and (4) clarify the physiological reasons for cultivar-specific AsA retention. We hypothesized that rapid AsA loss in high-AsA cultivars (e.g., ‘Hongyang’) is caused by a collapse of biosynthetic capacity combined with insufficient recycling, whereas stable AsA retention (e.g., ‘Guihai No.4’) depends on coordinated maintenance of GGP/GalLDH activity and efficient APX/MDHAR-mediated regeneration.

2. Materials and Methods

2.1 Subsection

The experimental materials were obtained from the kiwifruit germplasm repository of the Guangxi Institute of Botany. The cultivars used included: ‘Hongyang’ (*Actinidia chinensis* cv. Hongyang), ‘Guihai No.4’ (*Actinidia deliciosa* cv. Guihai No.4), and ‘Guihong’ (*Actinidia chinensis* cv. Guihong). Fruits were harvested at comparable physiological maturity. Fruits with uniform size, normal shape, no mechanical injury and no visible pest or disease symptoms were selected for the experiment..

2.2 Postharvest ripening treatment and sampling design

After harvest, fruits were transported to the laboratory and randomly divided into biological replicate groups. The fruits were stored at $(20 \pm 1)^{\circ}\text{C}$ and 85–90% relative humidity(RH) to simulate shelf-ripening conditions. Samples were collected at 0, 2, 4, 6 and 8 days. At each sampling point, firmness, total soluble solids (TSS), titratable acidity (TA), ethylene production and respiration rate were measured.

Mesocarp tissue was frozen immediately in liquid nitrogen and stored at -80°C for vitamin C and enzyme activity assays. Each biological replicate consisted of five fruits, and three biological replicates were used for each cultivar and sampling time.

2.3 Measurement of fruit quality indices

Fruit firmness was measured after peeling using a GY-4 fruit firmness tester and expressed as kg/cm². TSS was measured using a handheld refractometer and expressed as %. TA was determined by NaOH titration and expressed as citric acid equivalent. Ethylene production was measured by gas chromatography after fruits were sealed in airtight containers for 2h. Respiration rate was determined by measuring CO₂ release and expressed as mg.CO₂.kg⁻¹.h⁻¹..

2.4 Vitamin C and enzyme activity assays

Vitamin C, expressed as reduced ascorbic acid (AsA), was determined using the 2,6-dichlorophenolindophenol (DCPIP) titrimetric method with minor modifications. Briefly, frozen mesocarp tissue (2.0 g) was ground in liquid nitrogen and homogenized with 8 mL of ice-cold oxalic acid–EDTA extraction solution containing 2% (w/v) oxalic acid and 1 mM EDTA. The homogenate was centrifuged at 12,000 × g for 15 min at 4°C, and the supernatant was filtered through filter paper. An aliquot of the extract was titrated with standardized DCPIP solution until a stable light-pink endpoint persisted for 15s. A standard curve was prepared using freshly prepared L-ascorbic acid standards, and AsA content was expressed as mg/100 g fresh weight (FW).

For enzyme assays, frozen mesocarp tissue (2.0 g) was homogenized on ice with 8 mL of pre-cooled extraction buffer containing 50 mM potassium phosphate buffer (pH 7.5), 1 mM EDTA, 1 mM dithiothreitol (DTT), 0.1% (v/v) Triton X-100, 2% (w/v) polyvinylpyrrolidone (PVP), and 5% (v/v) glycerol. The homogenate was centrifuged at 12,000 × g for 20 min at 4°C, and the supernatant was used immediately as the crude enzyme extract. All spectrophotometric assays were performed at 25°C unless otherwise stated. Blank reactions without substrate or without enzyme extract were included to correct for non-enzymatic reactions. Protein concentration in the crude enzyme extract was determined by the Bradford method using bovine serum albumin as the standard. Enzyme activities were expressed as U/mg protein, where one unit (U) was defined as the amount of enzyme catalyzing the formation or consumption of 1 μmol of substrate or product per minut..

2.5 Statistical analysis

Data were analyzed using one-way analysis of variance (ANOVA) to evaluate differences among cultivars at each sampling day. Prior to ANOVA, data normality and homogeneity of variance were assessed using the Shapiro–Wilk test and Levene’s test, respectively. When ANOVA indicated significant differences, pairwise comparisons were performed using Tukey’s honestly significant difference (HSD) test, with significance set at $p < 0.05$. For correlation analysis, Pearson correlation coefficients were calculated to evaluate linear relationships between vitamin C content and enzyme activities after confirming approximate normal distribution of the variables. If the normality assumption was not met, Spearman’s

rank correlation analysis was used instead. For multiple correlation tests, p-values were adjusted using the Bonferroni correction to control for multiple comparisons. Results are presented as the mean $\pm$ standard deviation of three biological replicates. Figures were prepared using Origin software. The color key is consistent across all figures: black = 'Hongyang', gray = 'Guihong', and light yellow = 'Guihai No.4'. In all figure captions, different lowercase letters indicate significant differences among cultivars at the same sampling day based on Tukey's HSD test ($p < 0.05$).

3. Results and Discussion

3.1 cultivar-specific ripening behavior: softening, ethylene and respiration

During postharvest ripening at 20°C, fruit firmness declined in all three cultivars but at markedly different rates (Fig. 2a). 'Hongyang' softened rapidly, reaching the edible threshold ($\sim 1.5 \text{ kg}\cdot\text{cm}^{-2}$) by day 6, whereas 'Guihai No.4' softened slowly and only fell below the threshold on day 8; 'Guihong' showed an intermediate softening rate. Total soluble solids (TSS) increased gradually and titratable acidity (TA) decreased in all cultivars, with 'Hongyang' exhibiting the fastest changes (Fig. 2b, c). Ethylene production and respiration followed climacteric patterns (Fig. 2d, e): 'Hongyang' showed the earliest and highest ethylene peak (day 4), followed by 'Guihong', while 'Guihai No.4' exhibited the latest and lowest peak (day 6). Respiration rates peaked synchronously with ethylene, with 'Hongyang' again having the highest peak. These pronounced differences reflect distinct genetic backgrounds. 'Hongyang' rapidly enters the autocatalytic ethylene phase, accelerating cell wall degradation and softening (Atkinson et al., 2011). In contrast, 'Guihai No.4' shows lower ethylene sensitivity and a delayed climacteric rise, traits associated with extended storability in cultivars like 'Hayward' (Park et al., 2006; Mworio et al., 2010; Han et al., 2024). 'Guihong' displayed intermediate behavior, suggesting a mix of regulatory alleles that modulate ethylene signaling. These results confirm that genotype is the intrinsic determinant of postharvest ripening trajectories, consistent with reports that softening and ethylene peaks can be temporally uncoupled (Schroder & Atkinson, 2006; Mitalo et al., 2019).

3.2 Dynamic changes in vitamin C content and the role of biosynthetic enzymes

Initial AsA content varied considerably among genotypes (Fig. 3a). 'Hongyang' had the highest initial AsA ($\sim 120 \text{ mg}\cdot 100 \text{ g}^{-1} \text{ FW}$), followed by 'Guihai No.4' (~ 70) and 'Guihong' (~ 50). During ripening, 'Hongyang' lost approximately 40% of its AsA by day 6 (full softening stage). In contrast, 'Guihai No.4' maintained stable AsA levels during the first 4 days before a gradual decline, while 'Guihong' showed a continuous decline throughout ripening with no detectable accumulation phase. GGP activity closely paralleled these AsA dynamics (Fig. 3b): 'Hongyang' exhibited the highest GGP activity at harvest, followed by a rapid decline postharvest that synchronized with the sharp AsA loss. 'Guihai No.4' maintained relatively high GGP activity during early ripening, corresponding to its stable AsA phase. 'Guihong' consistently showed

the lowest GGP activity. GalLDH activity followed a similar pattern (Fig. 3c): ‘Hongyang’ had high initial activity that decreased quickly, whereas ‘Guihai No.4’ retained higher GalLDH activity during mid-ripening. The rapid AsA loss in ‘Hongyang’ despite high initial content indicates that postharvest stability depends on sustained biosynthetic flux rather than harvest-stage accumulation alone. GGP is the rate-limiting enzyme of the Smirnoff-Wheeler pathway (Wheeler et al., 1998; Bulley & Laing, 2016), and its decline in ‘Hongyang’ likely reflects feedback inhibition by high AsA via uORF-mediated translational control (Laing et al., 2015). In addition, the ethylene response factor AcERF91 has been shown to directly bind the GGP promoter and positively regulate its expression in kiwifruit (Chen et al., 2021); therefore, the rapid ethylene rise and subsequent signaling changes in ‘Hongyang’ may also contribute to GGP downregulation. Moreover, the rapid decay of GalLDH—the terminal mitochondrial enzyme (Bartoli et al., 2000; Leferink et al., 2008)—may compromise both AsA synthesis and mitochondrial redox homeostasis. The sustained GalLDH activity in ‘Guihai No.4’ suggests better preservation of mitochondrial function, which has been linked to lower oxidative stress (Alhagdow et al., 2007; Schimmeyer et al., 2016). Thus, cultivar differences in the postharvest maintenance of GGP and GalLDH are primary determinants of AsA retention.

3.3 The AsA-GSH recycling system: APX and MDHAR as key players

APX and MDHAR activities showed strong genotype-dependent patterns (Fig. 4a,b). ‘Guihai No.4’ exhibited clearly higher APX and MDHAR activities than ‘Hongyang’ and ‘Guihong’ throughout most of the ripening period. Pearson correlation analysis across all samples revealed strong positive relationships between APX activity and AsA content ($r = 0.82$) and between MDHAR activity and AsA content ($r = 0.76$) (Fig. 5). DHAR and GR activities showed relatively minor inter-cultivar differences, although ‘Hongyang’ exhibited a faster decline in GR activity during late ripening (Fig. 4c,d). The strong positive correlations indicate that efficient regeneration of AsA from its oxidized forms is critical for preventing net AsA loss. The AsA-GSH cycle—where APX scavenges H_2O_2 using AsA and MDHAR rapidly reduces monodehydroascorbate back to AsA—is a central antioxidant mechanism (Noctor & Foyer, 1998; Foyer & Noctor, 2011). In ‘Guihai No.4’, sustained high APX and MDHAR activities effectively mitigate oxidative stress and recycle AsA, thereby maintaining stable vitamin C levels. This is consistent with findings in cold-stored mango (Vithana et al., 2025) and kiwifruit (Chen et al., 2020), where upregulation of the AsA-GSH cycle preserves nutritional quality. The relatively lower recycling capacity in ‘Hongyang’, combined with its high ethylene-driven respiratory burst, creates a “double jeopardy” situation: accelerated AsA consumption cannot be compensated by regeneration. The faster decline of GR in ‘Hongyang’ may further limit the supply of reduced glutathione needed for DHA reduction (Gill & Tuteja, 2010). Consequently, robust recycling capacity—particularly APX and MDHAR—is a key determinant of postharvest AsA stability.

3.4 Integrating synthesis, recycling and ethylene intensity into a mechanistic model

Integrating the data reveals two contrasting mechanisms. ‘Hongyang’ combines high initial AsA (~ 120) with a rapid decline in GGP and GalLDH activities and only moderate APX/MDHAR levels, leading to approximately 40% net AsA loss by full softening. ‘Guihai No.4’ pairs moderate initial AsA (~ 70) with sustained GGP/GalLDH activities and high APX/MDHAR activities, resulting in stable AsA during early ripening and only a gradual decline thereafter. ‘Guihong’ has low initial AsA (~ 50), low biosynthetic enzyme activities, and low recycling capacity, thus consistently low AsA throughout. These results demonstrate that postharvest AsA retention is governed by the balance among three interacting factors: (i) ethylene-driven metabolic intensity (which determines oxidative pressure), (ii) the capacity for de novo AsA synthesis via GGP and GalLDH, and (iii) the efficiency of AsA regeneration through APX and MDHAR. This tripartite framework aligns with the emerging concept that ascorbic acid functions as a master redox regulator during fruit ripening, modulating both oxidative stress responses and metabolic transitions (Arabia et al., 2024). ‘Hongyang’ suffers from a collapse of synthesis and insufficient recycling, leading to rapid AsA depletion. In contrast, ‘Guihai No.4’ combines a naturally lower ethylene output (reduced oxidative load) with superior recycling machinery, allowing it to preserve AsA.. These findings have practical implications. For high-AsA but short-shelf-life cultivars like ‘Hongyang’, postharvest interventions that suppress ethylene (e.g., 1-MCP, cold storage) are likely to preserve AsA by reducing both consumption and the feedback suppression of GGP (Zhang et al., 2021; Ilina et al., 2010). For ‘Guihai No.4’, which already exhibits strong AsA retention, storage strategies should focus on preventing textural disorders and very-long-term senescence. From a breeding perspective, selecting for sustained GGP and GalLDH expression combined with high APX and MDHAR activities could yield kiwifruit varieties that combine high vitamin C at harvest with excellent postharvest stability. Recent genomic and transcriptomic resources in *Actinidia* (Huang et al., 2023; Liu et al., 2022) provide tools to identify such combined traits.

4. Conclusion

This study demonstrates that postharvest vitamin C stability in kiwifruit is determined by the coordinated regulation of biosynthesis and recycling pathways rather than initial AsA accumulation. A mechanistic model is proposed in which ethylene-driven metabolic intensity suppresses biosynthetic enzyme activities (GGP and GalLDH) while oxidative pressure is mitigated by the AsA–GSH recycling system, particularly APX and MDHAR. Cultivars with strong recycling capacity (e.g., ‘Guihai No.4’) maintain higher vitamin C stability, while cultivars with rapid ethylene response (e.g., ‘Hongyang’) experience accelerated AsA depletion. These findings provide practical guidance for postharvest management and breeding strategies aimed at improving nutritional quality in kiwifruit.

Declarations

Author Contributions: Conceptualization, X.L. and W.F.; methodology, X.L.; software, Y.K.; validation, X.L. and G.J.; formal analysis, L.C.; investigation, L.W.; resources, J.Q.; data curation, W.F.; writing—original draft preparation, X.L.; writing—review and editing, X.L.; visualization, L.C.; supervision, W.F.; project

administration, Y.K.; funding acquisition, W.F. All authors have read and agreed to the published version of the manuscript.

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Figures



Figure 1

Kiwifruit cultivars used in the experiment: (a) 'Guihai No.4'; (b) 'Guihong'; (c) 'Hongyang'.

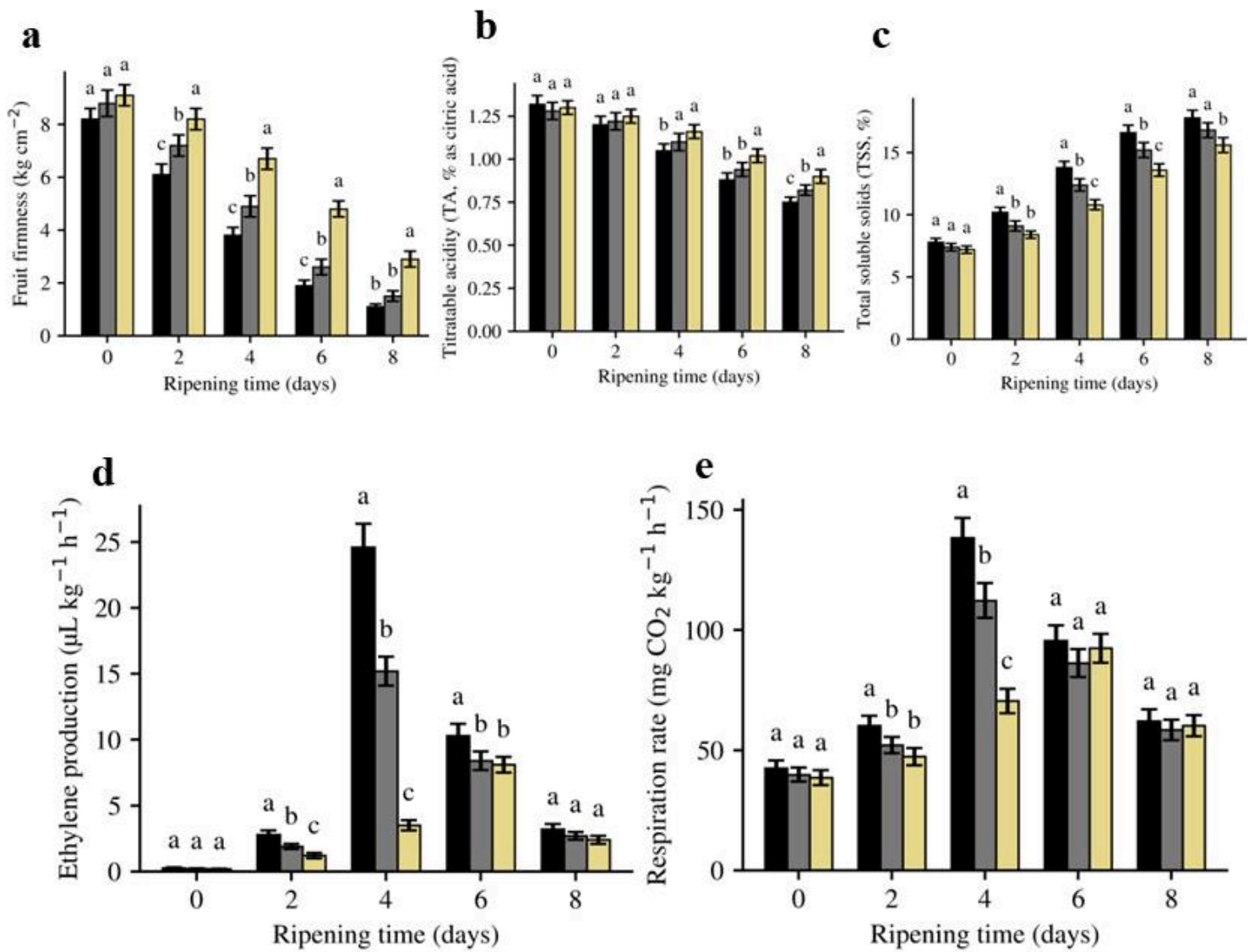


Figure 2

Postharvest ripening physiology of three kiwifruit cultivars: (a) fruit firmness; (b) total soluble solids (TSS); (c) titratable acidity (TA) ; (d) ethylene production rate; (e) CO_2 release rate.

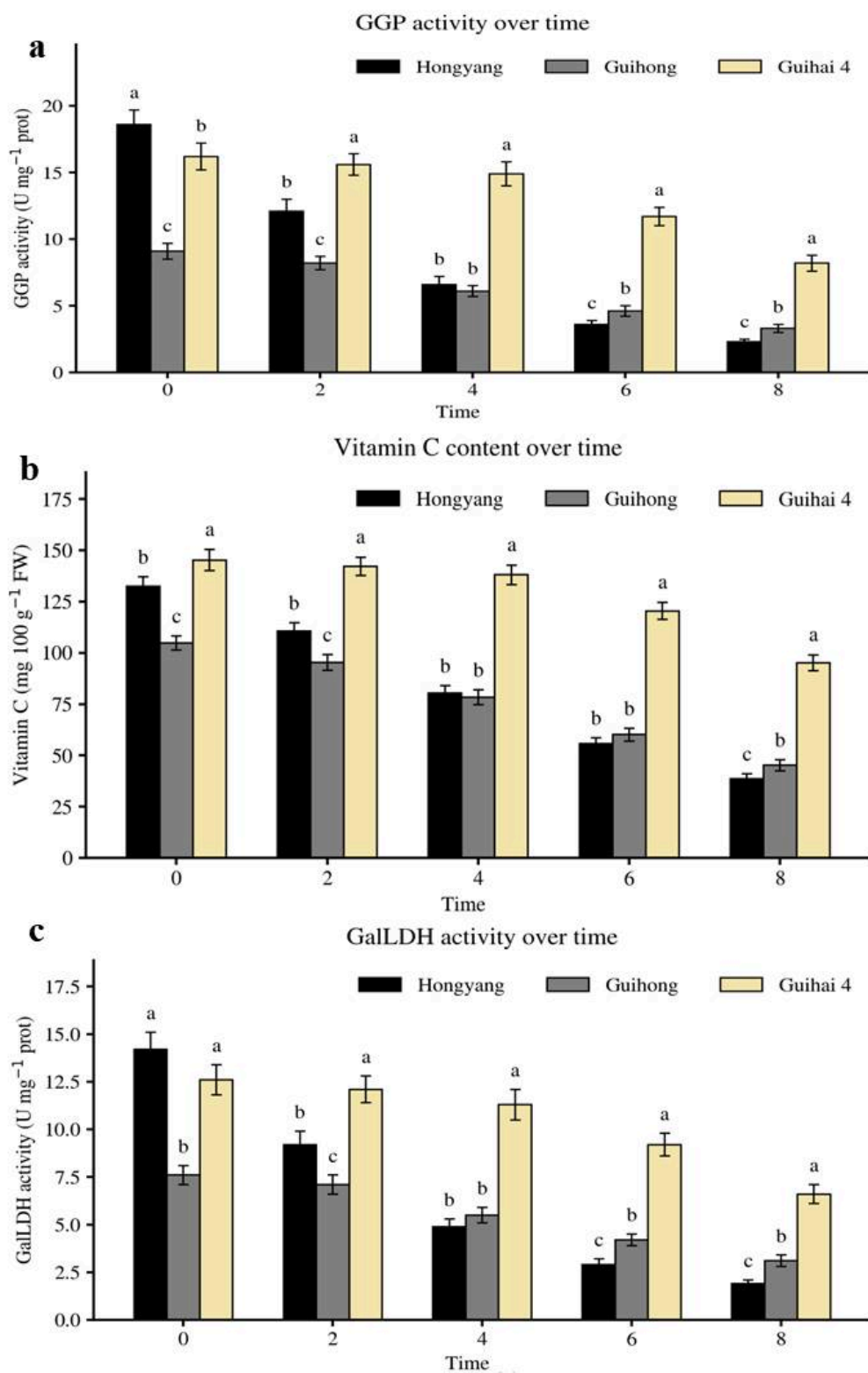


Figure 3

Dynamics of vitamin C and biosynthetic enzymes: (a) vitamin C; (b) GGP; (c) GalLDH.

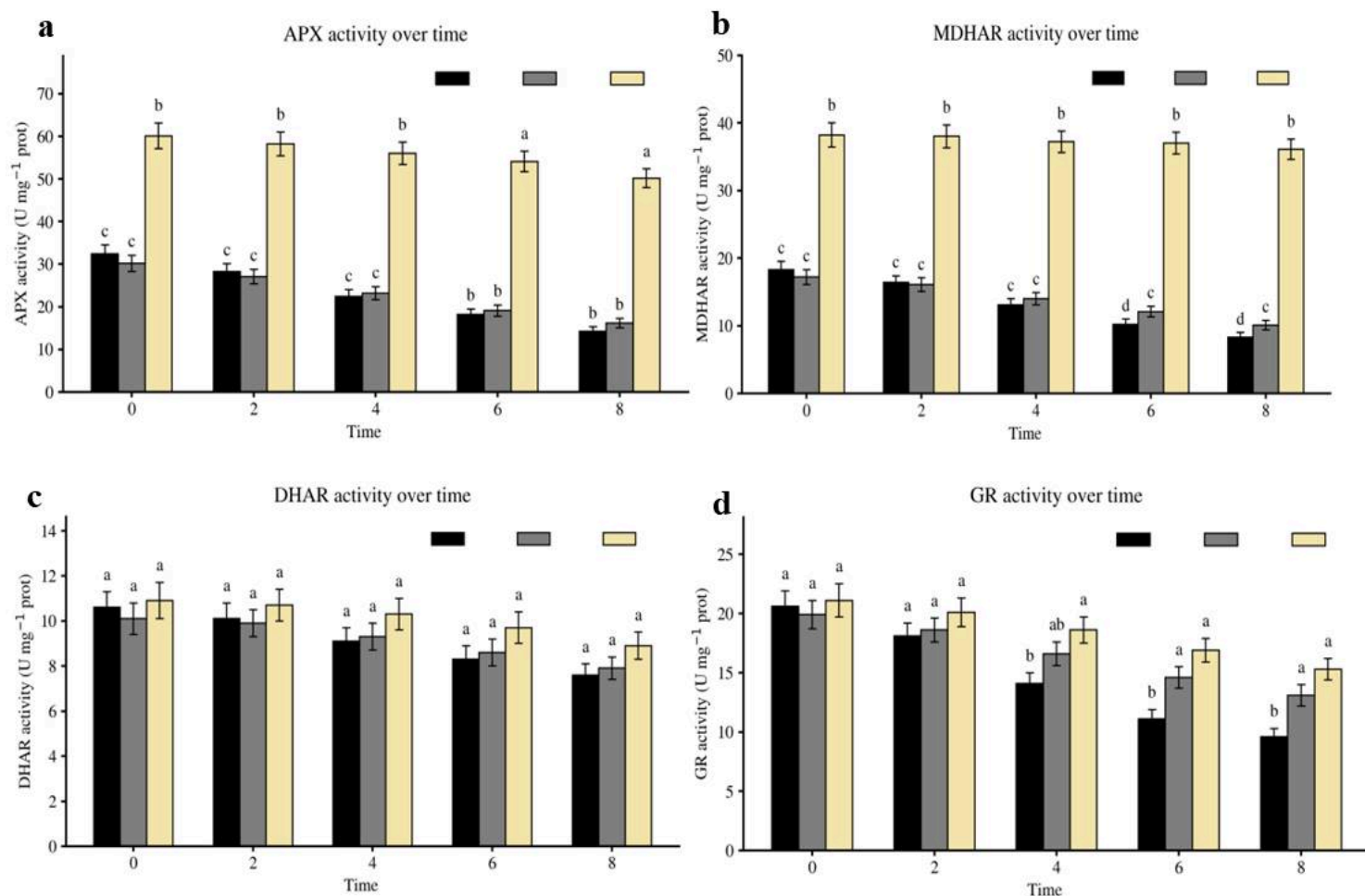


Figure 4

AsA-GSH cycle enzyme activities during postharvest ripening of three kiwifruit cultivars at 0, 2, 4, 6, and 8 days: (a) APX; (b) MDHAR; (c) DHAR; (d) GR.

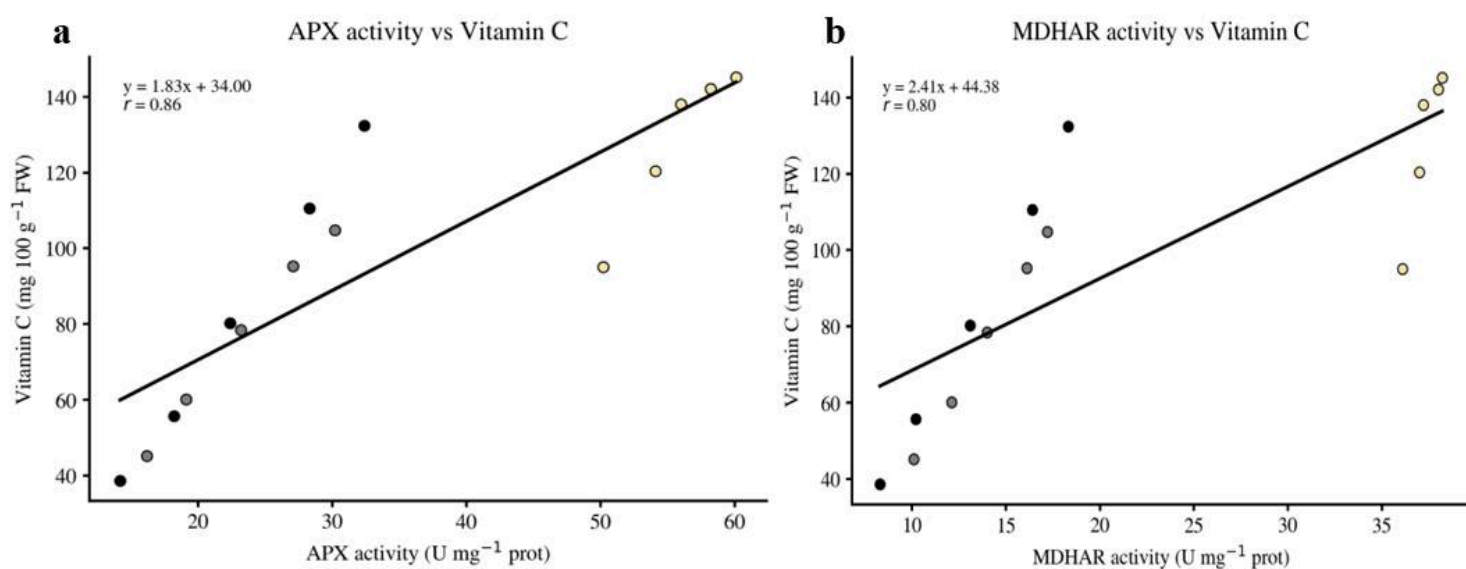


Figure 5

Integrated correlation between vitamin C and antioxidant enzyme system: (a) APX activity vs. vitamin C content; (b) MDHAR activity vs. vitamin C content.