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Tabish Jehan Been
Ph.D. Scholar, Division of Fruit Science, Sher-e-Kashmir University of Agricultural Science and Technology of Kashmir, Faculty of Horticulture, Shalimar, Srinagar, Jammu and Kashmir, India

Mohammad Amin Mir
Professor, Division of Fruit Science, Sher-e-Kashmir University of Agricultural Science and Technology of Kashmir, Faculty of Horticulture, Shalimar, Srinagar, Jammu and Kashmir, India

Ashaq Pandit
Professor and Head, Division of Fruit Science, Sher-e-Kashmir University of Agricultural Sciences and Technology, Faculty of Horticulture, Shalimar, Srinagar, Jammu and Kashmir, India

Abdul Raouf Malik
Assistant Professor, Division of Fruit Science, Sher-e- Kashmir University of Agricultural Science and Technology of Kashmir, Faculty of Horticulture, Shalimar, Srinagar, Jammu and Kashmir, India

Sajad Ahmed Bhat
Professor, Division of Basic Science and Humanities, Sher-e- Kashmir University of Agricultural Science and Technology of Kashmir, Faculty of Horticulture, Shalimar, Srinagar, Jammu and Kashmir, India

Sajad Majeed Zargar
Associate Professor, Division of Plant Biotechnology, Sher-e- Kashmir University of Agricultural Science and Technology of Kashmir, Faculty of Horticulture, Shalimar, Srinagar, Jammu and Kashmir, India

Arshad Hussain Mughal
Professor, Associate Director Research, Sher-e-Kashmir University of Agricultural Science and Technology of Kashmir, Faculty of Horticulture, Shalimar, Srinagar, Jammu and Kashmir, India

Iftisam Yaseen
Ph.D. Scholar, Division of Fruit Science, Sher-e-Kashmir University of Agricultural Science and Technology of Kashmir, Faculty of Horticulture, Shalimar, Srinagar, Jammu and Kashmir, India

Shaila Din
Ph.D. Scholar, Division of Fruit Science, Sher-e-Kashmir University of Agricultural Science and Technology of Kashmir, Faculty of Horticulture, Shalimar, Srinagar, Jammu and Kashmir, India

Nazish Farooq Mir
Msc Biodiversity Conservation, Division of Life and Environmental Sciences, Bournemouth Univeristy, BH125BB, (Bournmouth Dorset, United Kingdom

Dr. Khalid Mushtaq bhat
M.Sc., Biodiversity Conservation, Division of Life and Environmental Sciences, Bournemouth Univeristy, BH125BB, (Bournmouth Dorset, United Kingdom

Gazala Mansoor
M.Sc., Biodiversity Conservation, Division of Life and Environmental Sciences, Bournemouth Univeristy, BH125BB, (Bournmouth Dorset, United Kingdom

Corresponding Author:
Tabish Jehan Been
Division of Fruit Science, Faculty of Horticulture, Sher-e-Kashmir University of Agricultural Sciences and Technology of Kashmir, Srinagar, Jammu and Kashmir, India

Biochemical regulation of apple fruit russeting: Phenolic dynamics, antioxidant activity and the role of growth regulators

Tabish Jehan Been, Mohammad Amin Mir, Ashaq Pandit, Abdul Raouf Malik, Sajad Ahmed Bhat, Sajad Majeed Zargar, Arshad Hussain Mughal, Iftisam Yaseen, Shaila Din, Nazish Farooq Mir, Khalid Mushtaq Bhat and Gazala Mansoor

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Abstract
Fruit russeting is a major physiological disorder that adversely affects the external appearance and market acceptability of apple (*Malus domestica* Borkh.) fruits. The present investigation elucidates the biochemical regulation of russet development with particular emphasis on phenolic metabolism and antioxidant activity under the influence of different plant growth regulators. Two russet-susceptible apple cultivars, Red Velox and Golden Clone-B, were evaluated across successive stages of fruit development. Total phenols, flavonoids, flavonols and total antioxidant activity were quantified at five critical developmental stages. The results demonstrated a pronounced stage-dependent activation of phenylpropanoid metabolism during early fruit development, followed by a progressive decline toward harvest, whereas antioxidant activity increased consistently with fruit maturation. Treatments involving GA_{4+7} + 6-BA at optimal concentrations moderated early phenolic accumulation and were consistently associated with reduced russet expression, while higher concentrations of chlorogenic acid intensified phenolic accumulation and russet severity. Correlation analysis revealed a negative relationship between phenolic constituents and antioxidant activity at harvest, indicating a metabolic shift from structural reinforcement toward oxidative balance during fruit maturation. The study establishes a biochemical framework for russet development and provides a scientific basis for its management in apple.

Keywords: Apple russeting; Phenylpropanoid metabolism; Phenolic compounds; Flavonoids; Flavonols; Antioxidant activity

1. Introduction
1.1 Importance of apple and fruit surface quality
Apple (*Malus domestica* Borkh.) is one of the most widely cultivated and economically significant temperate fruit crops worldwide, contributing substantially to global fruit production and trade. Consumer acceptance of apple fruits is strongly influenced by external quality attributes, particularly fruit size, shape, colour uniformity and surface smoothness. In high-value fresh fruit markets, visual appearance often determines consumer preference and pricing, sometimes outweighing internal quality attributes such as flavour and nutritional composition. Consequently, surface-related physiological disorders pose a serious challenge to the commercial sustainability of apple production systems.

Among surface defects, fruit russeting is recognized as one of the most persistent and economically damaging disorders in apple cultivation. Even limited russet coverage can result in downgrading of fruits to lower market classes, thereby reducing grower profitability. This issue is particularly critical for dessert apple cultivars intended for premium domestic and export markets, where cosmetic quality standards are stringent.

1.2 Russeting as a physiological and developmental disorder
Russeting is characterized by the appearance of brown, rough and corky patches on the fruit surface, resulting from the replacement of the normal epidermis and cuticle by a suberized

periderm. Importantly, russeting is not associated with pathogenic infection but is classified as a physiological disorder influenced by a complex interaction of genetic, environmental and management-related factors. Environmental conditions such as prolonged surface wetness, high humidity, rainfall events, low temperatures and reduced solar radiation during early fruit development have been widely implicated in promoting russet formation.

From a developmental standpoint, russeting is initiated during early stages of fruit growth, when epidermal cells undergo rapid expansion and the cuticle is still thin and incompletely developed. Under these conditions, mechanical stress imposed by fruit enlargement, combined with environmental stressors, can disrupt cuticular integrity. Subsequent exposure of epidermal tissues triggers wound-like responses, culminating in periderm formation and visible russeting. Therefore, russeting should be regarded as a developmentally regulated process rather than a late-arising surface defect.

1.3 Phenolic metabolism and its association with russet development

Phenolic compounds constitute a major class of secondary metabolites in apple fruits and play essential roles in structural reinforcement, stress response and defense-related metabolism. These compounds include phenolic acids, flavonoids and flavonols, which collectively originate from the phenylpropanoid biosynthetic pathway. Activation of this pathway is commonly associated with tissue stress, wounding and suberization processes.

In apple fruits, enhanced accumulation of phenolic compounds in the peel has been repeatedly associated with russeted tissues. Phenolics contribute to cell wall lignification and suberin deposition, both of which are key structural components of periderm tissue. During early fruit development, when epidermal cells are highly responsive to physiological cues, excessive activation of phenylpropanoid metabolism may predispose the fruit surface to cuticular failure and subsequent russet formation. Consequently, temporal profiling of phenolic compounds provides critical insight into the biochemical mechanisms underlying russet initiation and progression.

1.4 Antioxidant activity and oxidative balance during fruit development

Fruit growth and maturation are accompanied by dynamic changes in cellular metabolism, including the generation of reactive oxygen species as by-products of respiration and other metabolic processes. Antioxidant systems play a central role in maintaining oxidative homeostasis and protecting cellular structures from oxidative damage. In apple fruits, phenolic compounds contribute substantially to antioxidant capacity; however, antioxidant activity reflects the integrated action of multiple biochemical constituents rather than phenolic concentration alone.

Alterations in antioxidant activity during fruit development may influence epidermal stability and stress tolerance, thereby indirectly affecting russet susceptibility. A comprehensive assessment of antioxidant activity alongside phenolic profiles is therefore essential to understand how biochemical balance is maintained or disrupted during critical stages of fruit development.

1.5 Influence of growth regulators and rationale of the study

Chemical regulation of fruit development through the application of plant growth regulators has emerged as a practical approach for managing russeting in apple. Compounds such as gibberellins, cytokinins and phenolic modulators are known to influence epidermal cell expansion, cuticle development and metabolic activity within the fruit peel. Gibberellins, in particular, have been reported to enhance cuticular integrity and reduce russet incidence when applied during early fruit development, whereas the effects of phenolic modulators remain less clearly defined.

Despite extensive research on russet management, information on stage-wise biochemical responses of apple fruit peel to different growth regulator treatments remains limited. In particular, there is a lack of integrated studies examining phenolic metabolism, flavonoid dynamics, flavonol accumulation and antioxidant activity across successive stages of fruit development.

Therefore, the present investigation was undertaken to elucidate the biochemical regulation of apple fruit russeting with specific emphasis on phenolic compounds and antioxidant activity under the influence of different russet management chemicals. The study focuses exclusively on the biochemical component of the doctoral research work and aims to provide a mechanistic basis for the development of effective russet management strategies.

2. Materials and Methods

2.1 Experimental material and treatments

The investigation was conducted on two apple cultivars, Red Velox and Golden Clone-B, known for their susceptibility to russeting. Different chemical sprays were applied as foliar treatments, including GA_{4+7} + 6-BA, GA_3 + 6-BA and chlorogenic acid at various concentrations, along with an untreated control.

2.2 Sampling stages

Fruit samples were collected at five stages of fruit development, *viz.*, 7 days after treatment, 21 days after treatment, 45 days after treatment, 20 days before harvest and at harvest. Fruit peel was separated, processed and used for biochemical analysis.

2.3 Estimation of biochemical parameters

Total phenols were estimated using the Folin–Ciocalteu method and expressed as mg g^{-1} fruit weight. Total flavonoids and flavonols were determined using standard spectrophotometric methods. Total antioxidant activity was estimated using the DPPH radical scavenging assay and expressed as percentage antioxidant activity.

2.4 Statistical analysis

The experimental data were subjected to appropriate statistical analysis to assess the significance of differences among treatments, cultivars and sampling stages.

3. Results
3.1 Total phenolic content

Table 1: Effect of various russet management PGRs on total phenols (mg GAE/gm of fruit weight) (21 days after treatment) of apple cvs. Red Velox and Golden Clone-B

Varieties \ Treatments	2022			2023			Pooled		
	Red Velox	Golden Clone-B	Mean	Red Velox	Golden Clone-B	Mean	Red Velox	Golden Clone-B	Mean
G0: Control	7.374	6.874	7.124	7.624	7.124	7.374	7.499	6.999	7.249
G1: GA_{4+7}+ 6-BA @ 5.5 ppm	6.905	6.406	6.656	7.152	6.688	6.920	7.029	6.547	6.788
G2: GA_{4+7} + 6-BA @ 11 ppm	6.743	6.248	6.496	6.666	6.505	6.586	6.705	6.377	6.541
G3: GA_{4+7} + 6-BA @ 21 ppm	6.508	6.004	6.256	6.752	6.252	6.502	6.630	6.128	6.379
G4: Chlorogenic acid @ 88.5ppm	7.229	6.722	6.976	7.474	6.970	7.222	7.352	6.846	7.099
G5: Chlorogenic acid @ 177 ppm	6.504	6.003	6.254	6.677	6.251	6.464	6.591	6.127	6.359
G6: Chlorogenic acid @ 354 ppm	7.506	7.009	7.258	7.758	7.264	7.500	7.632	7.137	7.384
G7: GA_3 + 6-BA @ 5.5 ppm	6.998	6.497	6.748	7.246	6.756	7.001	7.122	6.627	6.874
G8: GA_3 + 6-BA @ 11 ppm	6.823	6.325	6.574	7.063	6.589	6.826	6.943	6.457	6.700
G9: GA_3 + 6-BA @ 21 ppm	6.604	6.102	6.353	6.864	6.347	6.606	6.734	6.225	6.479
Mean	6.919	6.419		7.128	6.675		7.024	6.547	
C.D.($\leq$ 0.05)									
Russet management chemicals (G)	0.024			0.156			0.076		
Varieties (V)	0.011			0.070			0.034		
G x V	NS			NS			NS		

Table 2: Effect of various russet management PGRs on total phenols (mg GAE/gm of fruit weight) (45 days after treatment) of apple cvs. Red Velox and Golden Clone-B

Varieties \ Treatments	2022			2023			Pooled		
	Red Velox	Golden Clone-B	Mean	Red Velox	Golden Clone-B	Mean	Red Velox	Golden Clone-B	Mean
G0: Control	5.365	4.877	5.121	5.624	5.134	5.379	5.495	5.006	5.250
G1: GA_{4+7}+ 6-BA @ 5.5 ppm	4.952	4.405	4.679	5.165	4.682	4.924	5.059	4.544	4.801
G2: GA_{4+7} + 6-BA @ 11 ppm	4.744	4.246	4.495	4.992	4.516	4.574	4.868	4.381	4.625
G3: GA_{4+7} + 6-BA @ 21 ppm	4.493	4.009	4.251	4.746	4.241	4.494	4.620	4.125	4.372
G4: Chlorogenic acid @ 88.5ppm	5.222	4.725	4.974	5.463	4.963	5.213	5.343	4.844	5.093
G5: Chlorogenic acid @ 177 ppm	4.507	4.002	4.255	4.671	4.265	4.468	4.589	4.134	4.361
G6: Chlorogenic acid @ 354 ppm	5.505	5.001	5.253	5.765	5.284	5.525	5.635	5.143	5.389
G7: GA_3 + 6-BA @ 5.5 ppm	4.996	4.497	4.747	5.234	4.768	5.001	5.115	4.633	4.874
G8: GA_3 + 6-BA @ 11 ppm	4.829	4.328	4.579	5.055	4.596	4.826	4.942	4.462	4.702
G9: GA_3 + 6-BA @ 21 ppm	4.602	4.069	4.336	4.879	4.339	4.609	4.741	4.204	4.472
Mean	4.910	4.410		5.160	4.670		5.035	4.540	
C.D.($\leq$ 0.05)									
Russet management chemicals (G)	0.032			0.040			0.027		
Varieties (V)	0.014			0.018			0.012		
G x V	NS			NS			NS		

Table 3: Effect of various russet management PGRs on total phenols (mg GAE/gm of fruit weight) (20 days before harvest) of apple cvs. Red Velox and Golden Clone-B

Varieties \ Treatments	2022			2023			Pooled		
	Red Velox	Golden Clone-B	Mean	Red Velox	Golden Clone-B	Mean	Red Velox	Golden Clone-B	Mean
G0: Control	3.372	2.874	3.123	3.627	3.127	3.377	3.500	3.001	3.250
G1: GA_{4+7}+ 6-BA @ 5.5 ppm	2.903	2.406	2.655	3.156	2.658	2.907	3.030	2.532	2.781
G2: GA_{4+7} + 6-BA @ 11 ppm	2.744	2.243	2.494	2.992	2.499	2.746	2.868	2.371	2.620
G3: GA_{4+7} + 6-BA @ 21 ppm	2.506	2.005	2.256	2.753	2.256	2.505	2.630	2.131	2.380
G4: Chlorogenic acid @ 88.5ppm	3.228	2.724	2.976	3.474	2.972	3.223	3.351	2.848	3.100
G5: Chlorogenic acid @ 177 ppm	2.504	2.006	2.255	2.756	2.251	2.504	2.630	2.129	2.379
G6: Chlorogenic acid @ 354 ppm	3.506	3.002	3.254	3.754	3.252	3.503	3.630	3.127	3.379
G7: GA_3 + 6-BA @ 5.5 ppm	2.995	2.494	2.745	3.247	2.743	2.995	3.121	2.619	2.870
G8: GA_3 + 6-BA @ 11 ppm	2.828	2.322	2.575	3.079	2.572	2.826	2.954	2.447	2.700
G9: GA_3 + 6-BA @ 21 ppm	2.607	2.106	2.357	2.858	2.354	2.606	2.733	2.230	2.481
Mean	2.919	2.418		3.170	2.668		3.044	2.543	
C.D.($\leq$ 0.05)									
Russet management chemicals (G)	0.001			0.002			0.004		
Varieties (V)	0.001			0.001			0.002		
G x V	NS			NS			NS		

Table 4: Effect of various russet management PGRs on total phenols (mg GAE/gm of fruit weight) (at harvest) of apple cvs. Red Velox and Golden Clone-B

Varieties \ Treatments	2022			2023			Pooled		
	Red Velox	Golden Clone-B	Mean	Red Velox	Golden Clone-B	Mean	Red Velox	Golden Clone-B	Mean
G0: Control	3.261	2.777	3.019	3.527	3.027	3.277	3.394	2.902	3.148
G1: GA_{4+7}+ 6-BA @ 5.5 ppm	2.855	2.295	2.575	3.048	2.554	2.801	2.952	2.452	2.688
G2: GA_{4+7} + 6-BA @ 11 ppm	2.649	2.146	2.398	2.889	2.391	2.640	2.769	2.269	2.519
G3: GA_{4+7} + 6-BA @ 21 ppm	2.467	1.953	2.210	2.646	2.150	2.398	2.557	2.052	2.304
G4: Chlorogenic acid @ 88.5ppm	3.115	2.612	2.864	3.375	2.872	3.124	3.245	2.742	2.994
G5: Chlorogenic acid @ 177 ppm	2.403	1.904	2.154	2.654	2.153	2.404	2.529	2.029	2.279
G6: Chlorogenic acid @ 354 ppm	3.404	2.906	3.155	3.651	3.145	3.398	3.528	3.026	3.227
G7: GA_3 + 6-BA @ 5.5 ppm	2.886	2.387	2.637	3.132	2.636	2.884	3.009	2.512	2.760
G8: GA_3 + 6-BA @ 11 ppm	2.725	2.225	2.475	2.973	2.478	2.726	2.849	2.352	2.600
G9: GA_3 + 6-BA @ 21 ppm	2.458	2.003	2.231	2.757	2.259	2.508	2.608	2.131	2.369
Mean	2.822	2.321		3.065	2.567		2.944	2.444	
C.D.($\leq$ 0.05)									
Russet management chemicals (G)	0.092			0.028			0.049		
Varieties (V)	0.041			0.013			0.022		
G x V	NS			NS			NS		

Table 5: Effect of various russet management PGRs on total flavonoids (mg QE/gm of fruit weight) (7 days after treatment) of apple cvs. Red Velox and Golden Clone-B

Varieties \ Treatments	2022			2023			Pooled		
	Red Velox	Golden Clone-B	Mean	Red Velox	Golden Clone-B	Mean	Red Velox	Golden Clone-B	Mean
G0: Control	6.070	5.947	6.009	6.217	6.077	6.147	6.144	6.012	6.077
G1: GA_{4+7}+ 6-BA @ 5.5 ppm	5.822	5.684	5.753	5.925	5.755	5.840	5.874	5.720	5.796
G2: GA_{4+7} + 6-BA @ 11 ppm	5.735	5.595	5.665	5.876	5.733	5.805	5.806	5.665	5.734
G3: GA_{4+7} + 6-BA @ 21 ppm	5.558	5.496	5.527	5.693	5.562	5.628	5.626	5.529	5.577
G4: Chlorogenic acid @ 88.5ppm	5.997	5.852	5.925	6.132	5.994	6.063	6.065	5.923	5.993
G5: Chlorogenic acid @ 177 ppm	5.690	5.461	5.576	5.731	5.605	5.668	5.711	5.533	5.621
G6: Chlorogenic acid @ 354 ppm	6.156	6.013	6.085	6.284	6.151	6.218	6.220	6.082	6.151
G7: GA_3 + 6-BA @ 5.5 ppm	5.871	5.736	5.804	6.045	5.872	5.959	5.958	5.804	5.881
G8: GA_3 + 6-BA @ 11 ppm	5.701	5.635	5.668	5.971	5.773	5.872	5.836	5.704	5.770
G9: GA_3 + 6-BA @ 21 ppm	5.653	5.514	5.584	5.770	5.626	5.698	5.712	5.570	5.640
Mean	5.825	5.693		5.964	5.815		5.895	5.754	
C.D.($\leq$ 0.05)									
Russet management chemicals (G)	0.007			0.019			0.011		
Varieties (V)	0.003			0.008			0.005		
G x V	0.010			NS			NS		

Table 6: Effect of various russet management PGRs on total flavonoids (mg QE/gm of fruit weight) (21 days after treatment) of apple cvs. Red Velox and Golden Clone-B

Varieties \ Treatments	2022			2023			Pooled		
	Red Velox	Golden Clone-B	Mean	Red Velox	Golden Clone-B	Mean	Red Velox	Golden Clone-B	Mean
G0: Control	5.257	4.977	5.117	5.391	5.124	5.258	5.324	5.051	5.187
G1: GA_{4+7}+ 6-BA @ 5.5 ppm	4.995	4.725	4.860	5.134	4.875	5.005	5.065	4.800	4.932
G2: GA_{4+7} + 6-BA @ 11 ppm	4.903	4.633	4.768	4.865	4.776	4.821	4.884	4.705	4.794
G3: GA_{4+7} + 6-BA @ 21 ppm	4.771	4.502	4.637	4.916	4.643	4.780	4.844	4.573	4.708
G4: Chlorogenic acid @ 88.5ppm	5.175	4.891	5.033	5.370	5.032	5.201	5.273	4.962	5.117
G5: Chlorogenic acid @ 177 ppm	4.779	4.504	4.642	4.878	4.641	4.760	4.829	4.573	4.700
G6: Chlorogenic acid @ 354 ppm	5.324	4.056	5.190	5.464	5.194	5.329	5.394	5.125	5.259
G7: GA_3 + 6-BA @ 5.5 ppm	5.045	4.772	4.909	5.182	4.915	5.049	5.114	4.844	4.978
G8: GA_3 + 6-BA @ 11 ppm	4.956	4.677	4.817	5.083	4.817	4.950	5.020	4.747	4.883
G9: GA_3 + 6-BA @ 21 ppm	4.833	4.558	4.696	4.976	4.969	4.836	4.905	4.627	4.765
Mean	5.004	4.730		5.126	4.871		5.065	4.800	
C.D.($\leq$ 0.05)									
Russet management chemicals (G)	0.007			0.047			0.023		
Varieties (V)	0.003			0.021			0.010		
G x V	NS			NS			NS		

Table 7: Effect of various russet management PGRs on total flavonoids (mg QE/gm of fruit weight) (45 days after treatment) of apple cvs. Red Velox and Golden Clone-B

Varieties \ Treatments	2022			2023			Pooled		
	Red Velox	Golden Clone-B	Mean	Red Velox	Golden Clone-B	Mean	Red Velox	Golden Clone-B	Mean
G0: Control	3.414	2.777	3.096	4.287	4.027	4.157	3.851	3.402	3.626
G1: GA_{4+7}+ 6-BA @ 5.5 ppm	3.162	2.525	2.844	4.044	3.775	3.910	3.603	3.150	3.376
G2: GA_{4+7} + 6-BA @ 11 ppm	3.076	2.433	2.755	3.945	3.686	3.816	3.511	3.060	3.285
G3: GA_{4+7} + 6-BA @ 21 ppm	2.944	2.301	2.623	3.806	3.533	3.670	3.375	2.917	3.146
G4: Chlorogenic acid @ 88.5ppm	3.336	2.694	3.015	4.203	3.932	4.068	3.770	3.313	3.541
G5: Chlorogenic acid @ 177 ppm	2.943	2.350	2.647	3.762	3.541	3.652	3.353	2.946	3.149
G6: Chlorogenic acid @ 354 ppm	3.492	2.859	3.176	4.371	4.014	4.238	3.932	3.482	3.706
G7: GA_3 + 6-BA @ 5.5 ppm	3.214	2.578	2.896	4.074	3.827	3.951	3.644	3.203	3.423
G8: GA_3 + 6-BA @ 11 ppm	3.115	2.477	2.796	3.976	3.728	3.852	3.546	3.103	3.324
G9: GA_3 + 6-BA @ 21 ppm	2.996	2.356	2.676	3.889	3.589	3.739	3.443	2.973	3.207
Mean	3.169	2.535		4.036	3.774		3.602	3.155	
C.D.($\leq$ 0.05)									
Russet management chemicals (G)	0.010			0.012			0.008		
Varieties (V)	0.004			0.005			0.003		
G x V	NS			NS			NS		

Table 8: Effect of various russet management PGRs on total flavonoids (mg QE/gm of fruit weight) (20 days before harvest) of apple cvs. Red Velox and Golden Clone-B

Varieties \ Treatments	2022			2023			Pooled		
	Red Velox	Golden Clone-B	Mean	Red Velox	Golden Clone-B	Mean	Red Velox	Golden Clone-B	Mean
G0: Control	3.050	2.777	2.914	3.197	2.917	3.057	3.124	2.847	2.985
G1: GA_{4+7}+ 6-BA @ 5.5 ppm	2.797	2.525	2.661	2.935	2.654	2.795	2.866	2.590	2.727
G2: GA_{4+7} + 6-BA @ 11 ppm	2.708	2.433	2.571	2.846	2.565	2.706	2.777	2.499	2.638
G3: GA_{4+7} + 6-BA @ 21 ppm	2.579	2.301	2.440	2.719	2.436	2.578	2.649	2.369	2.508
G4: Chlorogenic acid @ 88.5ppm	2.975	2.694	2.835	3.108	2.833	2.971	3.042	2.764	2.902
G5: Chlorogenic acid @ 177 ppm	2.574	2.305	2.440	2.714	2.432	2.573	2.644	2.369	2.506
G6: Chlorogenic acid @ 354 ppm	3.126	2.859	2.993	3.266	2.981	3.124	3.196	2.920	3.058
G7: GA_3 + 6-BA @ 5.5 ppm	2.842	2.576	2.709	2.973	2.706	2.840	2.908	2.641	2.774
G8: GA_3 + 6-BA @ 11 ppm	2.751	2.473	2.612	2.882	2.615	2.749	2.817	2.544	2.680
G9: GA_3 + 6-BA @ 21 ppm	2.632	2.352	2.492	2.761	2.494	2.628	2.697	2.423	2.559
Mean	2.803	2.530		2.940	2.663		2.872	2.596	
C.D.($\leq$ 0.05)									
Russet management chemicals (G)	0.002			0.004			0.002		
Varieties (V)	0.001			0.002			0.001		
G x V	NS			NS			NS		

Table 9: Effect of various russet management PGRs on total flavonoids (mg QE/gm of fruit weight) (at harvest) of apple cvs. Red Velox and Golden Clone-B

Varieties \ Treatments	2022			2023			Pooled		
	Red Velox	Golden Clone-B	Mean	Red Velox	Golden Clone-B	Mean	Red Velox	Golden Clone-B	Mean
G0: Control	2.997	2.727	2.862	3.137	2.867	3.002	3.067	2.797	2.932
G1: GA_{4+7}+ 6-BA @ 5.5 ppm	2.768	2.468	2.618	2.878	2.608	2.743	2.823	2.538	2.680
G2: GA_{4+7} + 6-BA @ 11 ppm	2.659	2.379	2.519	2.789	2.519	2.654	2.724	2.449	2.586
G3: GA_{4+7} + 6-BA @ 21 ppm	2.556	2.276	2.416	2.656	2.386	2.521	2.606	2.331	2.468
G4: Chlorogenic acid @ 88.5ppm	2.915	2.635	2.775	3.055	2.775	2.915	2.985	2.705	2.845
G5: Chlorogenic acid @ 177 ppm	2.524	2.244	2.384	2.654	2.384	2.519	2.589	2.314	2.451
G6: Chlorogenic acid @ 354 ppm	3.072	2.793	2.933	3.230	2.932	3.081	3.151	2.863	3.006
G7: GA_3 + 6-BA @ 5.5 ppm	2.783	2.512	2.648	2.922	2.653	2.788	2.853	2.583	2.717
G8: GA_3 + 6-BA @ 11 ppm	2.691	2.421	2.556	2.833	2.552	2.693	2.762	2.487	2.624
G9: GA_3 + 6-BA @ 21 ppm	2.542	2.302	2.422	2.712	2.431	2.572	2.627	2.367	2.496
Mean	2.751	2.476		2.887	2.611		2.819	2.543	
C.D.($\leq$ 0.05)									
Russet management chemicals (G)	0.028			0.008			0.015		
Varieties (V)	0.012			0.004			0.007		
G x V	NS			NS			NS		

Table 10: Effect of various russet management PGRs on total flavonols (mg QE/gm of fruit weight) (7 days after treatment) of apple cvs. Red Velox and Golden Clone-B

Varieties \ Treatments	2022			2023			Pooled		
	Red Velox	Golden Clone-B	Mean	Red Velox	Golden Clone-B	Mean	Red Velox	Golden Clone-B	Mean
G0: Control	5.012	4.747	4.880	5.157	4.877	5.017	5.085	4.812	4.948
G1: GA_{4+7}+ 6-BA @ 5.5 ppm	4.754	4.484	4.619	4.898	4.555	4.727	4.826	4.520	4.672
G2: GA_{4+7} + 6-BA @ 11 ppm	4.675	4.395	4.535	4.809	4.533	4.671	4.742	4.464	4.603
G3: GA_{4+7} + 6-BA @ 21 ppm	4.536	4.266	4.401	4.676	4.401	4.539	4.606	4.334	4.469
G4: Chlorogenic acid @ 88.5ppm	4.939	4.653	4.796	5.075	4.794	4.935	5.007	4.724	4.865
G5: Chlorogenic acid @ 177 ppm	4.538	4.262	4.400	4.674	4.405	4.540	4.606	4.334	4.469
G6: Chlorogenic acid @ 354 ppm	5.087	4.811	4.949	5.221	4.959	5.090	5.154	4.885	5.019
G7: GA_3 + 6-BA @ 5.5 ppm	4.805	4.532	4.669	4.942	4.678	4.810	4.874	4.605	4.739
G8: GA_3 + 6-BA @ 11 ppm	4.716	4.436	4.576	4.853	4.576	4.715	4.785	4.506	4.645
G9: GA_3 + 6-BA @ 21 ppm	4.593	4.315	4.454	4.733	4.423	7.578	4.663	4.369	4.516
Mean	4.766	4.490		4.904	4.620		4.835	4.555	
C.D.(≤ 0.05)									
Russet management chemicals (G)	0.013			0.034			0.019		
Varieties (V)	0.006			0.015			0.009		
G x V	0.019			0.020			0.023		

Table 11: Effect of various russet management PGRs on total flavonols (mg QE/gm of fruit weight) (21 days after treatment) of apple cvs. Red Velox and Golden Clone-B

Varieties \ Treatments	2022			2023			Pooled		
	Red Velox	Golden Clone-B	Mean	Red Velox	Golden Clone-B	Mean	Red Velox	Golden Clone-B	Mean
G0: Control	4.057	3.777	3.917	4.191	3.927	4.059	4.124	3.852	3.988
G1: GA_{4+7}+ 6-BA @ 5.5 ppm	3.795	3.528	3.662	3.935	3.675	3.805	3.865	3.602	3.733
G2: GA_{4+7} + 6-BA @ 11 ppm	3.704	3.439	3.572	3.666	3.576	3.621	3.685	3.508	3.596
G3: GA_{4+7} + 6-BA @ 21 ppm	3.572	3.305	3.439	3.719	3.449	3.584	3.646	3.377	3.511
G4: Chlorogenic acid @ 88.5ppm	3.971	3.691	3.831	4.108	3.838	3.973	4.040	3.765	3.902
G5: Chlorogenic acid @ 177 ppm	3.571	3.304	3.438	3.677	3.444	3.561	3.624	3.374	3.499
G6: Chlorogenic acid @ 354 ppm	4.122	3.855	3.989	4.264	3.991	4.128	4.193	3.923	4.058
G7: GA_3 + 6-BA @ 5.5 ppm	3.846	3.576	3.711	3.985	3.712	3.849	3.916	3.644	3.779
G8: GA_3 + 6-BA @ 11 ppm	3.754	3.473	3.614	3.886	3.613	3.750	3.820	3.543	3.681
G9: GA_3 + 6-BA @ 21 ppm	3.635	3.352	3.494	3.773	3.492	3.633	3.704	3.422	3.563
Mean	3.803	3.530		3.920	3.672		3.862	3.601	
C.D.(≤ 0.05)									
Russet management chemicals (G)	0.013			0.086			0.042		
Varieties (V)	0.006			0.038			0.019		
G x V	NS			NS			NS		

Table 12: Effect of various russet management PGRs on total flavonols (mg QE/gm of fruit weight) (20 days before harvest) of apple cvs. Red Velox and Golden Clone-B

Varieties \ Treatmens	2022			2023			Pooled		
	Red Velox	Golden Clone-B	Mean	Red Velox	Golden Clone-B	Mean	Red Velox	Golden Clone-B	Mean
G0: Control	2.217	1.577	1.897	3.087	2.827	2.957	2.652	2.202	2.427
G1: GA_{4+7}+ 6-BA @ 5.5 ppm	1.965	1.325	1.645	2.845	2.575	2.710	2.405	1.950	2.177
G2: GA_{4+7} + 6-BA @ 11 ppm	1.876	1.233	1.555	2.743	2.488	2.616	2.310	1.861	2.085
G3: GA_{4+7} + 6-BA @ 21 ppm	1.743	1.102	1.423	2.602	2.339	2.471	2.173	1.721	1.946
G4: Chlorogenic acid @ 88.5ppm	2.132	1.491	1.812	3.001	2.736	2.869	2.567	2.114	2.340
G5: Chlorogenic acid @ 177 ppm	1.741	1.104	1.423	2.564	2.343	2.454	2.153	1.724	1.938
G6: Chlorogenic acid @ 354 ppm	2.294	1.658	1.976	3.175	2.902	3.039	2.735	2.280	2.507
G7: GA_3 + 6-BA @ 5.5 ppm	2.015	1.379	1.697	2.876	2.621	2.749	2.446	2.000	2.222
G8: GA_3 + 6-BA @ 11 ppm	1.916	1.276	1.569	2.779	2.524	2.652	2.348	1.900	2.123
G9: GA_3 + 6-BA @ 21 ppm	1.799	1.153	1.476	2.688	2.383	5.536	2.244	1.768	2.006
Mean	1.970	1.330		2.836	2.574		2.403	1.952	
C.D.(≤ 0.05)									
Russet management chemicals (G)	0.381			0.022			0.015		
Varieties (V)	0.171			0.010			0.007		
G x V	NS			NS			NS		

Table 13: Effect of various russet management PGRs on total flavonols (mg QE/gm of fruit weight) (at harvest) of apple cvs. Red Velox and Golden Clone-B

Varieties \ Treatments	2022			2023			Pooled		
	Red Velox	Golden Clone-B	Mean	Red Velox	Golden Clone-B	Mean	Red Velox	Golden Clone-B	Mean
G0: Control	1.851	1.571	1.711	1.997	1.717	1.857	1.924	1.644	1.784
G1: GA_{4+7}+ 6-BA @ 5.5 ppm	1.592	1.322	1.457	1.734	1.454	1.594	1.663	1.388	1.525
G2: GA_{4+7} + 6-BA @ 11 ppm	1.503	1.233	1.368	1.645	1.365	1.505	1.574	1.299	1.436
G3: GA_{4+7} + 6-BA @ 21 ppm	1.376	1.106	1.241	1.516	1.236	1.376	1.446	1.171	1.308
G4: Chlorogenic acid @ 88.5ppm	1.775	1.495	1.635	1.903	1.633	1.768	1.839	1.564	1.701
G5: Chlorogenic acid @ 177 ppm	1.374	1.104	1.239	1.512	1.232	1.372	1.443	1.168	1.305
G6: Chlorogenic acid @ 354 ppm	1.927	1.657	1.792	2.061	1.781	1.921	1.994	1.719	1.856
G7: GA_3 + 6-BA @ 5.5 ppm	1.648	1.378	1.513	1.772	1.502	1.637	1.710	1.440	1.575
G8: GA_3 + 6-BA @ 11 ppm	1.559	1.279	1.419	1.683	1.413	1.548	1.621	1.346	1.483
G9: GA_3 + 6-BA @ 21 ppm	1.436	1.156	1.296	1.562	1.296	1.429	1.499	1.226	1.362
Mean	1.604	1.330		1.739	1.463		1.671	1.397	
C.D.(≤ 0.05)									
Russet management chemicals (G)	0.002			0.004			0.002		
Varieties (V)	0.001			0.002			0.001		
G x V	NS			NS			NS		

Table 14: Effect of various russet management PGRs on total flavonols (mg QE/gm of fruit weight) (at harvest) of apple cvs. Red Velox and Golden Clone-B

Varieties \ Treatments	2022			2023			Pooled		
	Red Velox	Golden Clone-B	Mean	Red Velox	Golden Clone-B	Mean	Red Velox	Golden Clone-B	Mean
G0: Control	1.797	1.527	1.662	1.937	1.661	1.799	1.867	1.594	1.730
G1: GA_{4+7}+ 6-BA @ 5.5 ppm	1.565	1.268	1.417	1.675	1.405	1.540	1.620	1.337	1.478
G2: GA_{4+7} + 6-BA @ 11 ppm	1.452	1.179	1.316	1.583	1.319	1.451	1.518	1.249	1.383
G3: GA_{4+7} + 6-BA @ 21 ppm	1.354	1.075	1.215	1.456	1.188	1.322	1.405	1.132	1.268
G4: Chlorogenic acid @ 88.5ppm	1.715	1.434	1.575	1.859	1.577	1.718	1.787	1.506	1.646
G5: Chlorogenic acid @ 177 ppm	1.329	1.041	1.185	1.458	1.184	1.321	1.394	1.113	1.253
G6: Chlorogenic acid @ 354 ppm	1.878	1.597	1.738	2.005	1.735	1.870	1.942	1.666	1.803
G7: GA_3 + 6-BA @ 5.5 ppm	1.587	1.318	1.453	1.724	1.456	1.590	1.656	1.387	1.521
G8: GA_3 + 6-BA @ 11 ppm	1.495	1.222	1.359	1.631	1.353	1.492	1.563	1.288	1.425
G9: GA_3 + 6-BA @ 21 ppm	1.346	1.103	1.225	1.512	1.232	1.372	1.429	1.168	1.298
Mean	1.552	1.276		1.684	1.411		1.618	1.344	
C.D.(≤ 0.05)									
Russet management chemicals (G)	0.051			0.015			0.027		
Varieties (V)	0.023			0.007			0.012		
G x V	NS			NS			NS		

Table 15: Effect of various russet management PGRs on total antioxidant activity (%) (7 days after treatment) of apple cvs. Red Velox and Golden Clone-B

Varieties \ Treatments	2022			2023			Pooled		
	Red Velox	Golden Clone-B	Mean	Red Velox	Golden Clone-B	Mean	Red Velox	Golden Clone-B	Mean
G0: Control	18.89	20.20	19.55	18.40	19.71	19.06	18.64	19.95	19.30
G1: GA_{4+7}+ 6-BA @ 5.5 ppm	19.42	20.81	20.10	18.91	20.31	19.61	19.15	20.55	19.85
G2: GA_{4+7} + 6-BA @ 11 ppm	20.42	21.45	20.90	19.91	20.13	20.41	20.15	21.15	20.65
G3: GA_{4+7} + 6-BA @ 21 ppm	21.04	22.02	21.52	20.55	21.51	21.03	20.79	21.75	21.27
G4: Chlorogenic acid @ 88.5ppm	19.01	20.30	19.66	18.52	19.81	19.17	18.76	20.05	19.41
G5: Chlorogenic acid @ 177 ppm	21.21	22.57	21.89	20.72	22.08	21.40	20.96	22.32	21.64
G6: Chlorogenic acid @ 354 ppm	18.91	20.34	19.62	18.42	19.85	19.13	18.66	20.09	19.37
G7: GA_3 + 6-BA @ 5.5 ppm	18.86	20.59	19.73	18.37	20.16	19.24	18.61	20.34	19.48
G8: GA_3 + 6-BA @ 11 ppm	19.79	21.25	20.50	19.30	20.71	20.01	19.54	20.95	20.25
G9: GA_3 + 6-BA @ 21 ppm	20.59	21.79	21.19	20.10	21.38	20.70	20.34	21.54	20.94
Mean	19.81	21.12		19.71	20.63		19.56	20.87	
C.D.(≤ 0.05)									
Russet management chemicals (G)	0.177			0.177			0.177		
Varieties (V)	0.079			0.079			0.079		
G x V	0.250			0.250			0.250		

Table 16: Effect of various russet management PGRs on total antioxidant activity (%) (21 days after treatment) of apple cvs. Red Velox and Golden Clone-B

Varieties \ Treatments	2022			2023			Pooled		
	Red Velox	Golden Clone-B	Mean	Red Velox	Golden Clone-B	Mean	Red Velox	Golden Clone-B	Mean
G0: Control	26.90	28.51	27.70	26.04	27.52	26.78	26.47	28.01	27.24
G1: GA_{4+7}+ 6-BA @ 5.5 ppm	28.90	30.20	29.55	28.04	29.21	28.62	28.47	29.70	29.08
G2: GA_{4+7} + 6-BA @ 11 ppm	29.01	32.02	30.51	28.15	31.03	29.59	28.58	31.52	30.05
G3: GA_{4+7} + 6-BA @ 21 ppm	30.07	33.01	31.54	29.21	32.02	30.61	29.64	32.51	31.07
G4: Chlorogenic acid @ 88.5ppm	27.80	29.07	28.43	26.94	28.08	27.51	27.37	28.57	27.97
G5: Chlorogenic acid @ 177 ppm	30.76	33.33	32.04	29.90	32.34	31.12	30.33	32.83	31.58
G6: Chlorogenic acid @ 354 ppm	26.59	28.56	27.58	25.73	27.57	26.65	26.16	28.06	27.11
G7: GA_3 + 6-BA @ 5.5 ppm	28.40	29.67	29.00	27.54	28.61	28.07	27.97	29.10	28.53
G8: GA_3 + 6-BA @ 11 ppm	28.68	31.58	30.13	27.82	30.59	29.20	28.25	31.08	29.66
G9: GA_3 + 6-BA @ 21 ppm	29.50	32.55	31.00	28.64	31.51	30.07	29.07	32.00	30.53
Mean	28.66	30.84		27.80	29.55		28.23	30.34	
C.D.($\leq$ 0.05)									
Russet management chemicals (G)	0.107			0.110			0.108		
Varieties (V)	0.048			0.049			0.048		
G x V	0.151			0.156			0.153		

Table 17: Effect of various russet management PGRs on total antioxidant activity (%) (45 days after treatment) of apple cvs. Red Velox and Golden Clone-B

Varieties \ Treatments	2022			2023			Pooled		
	Red Velox	Golden Clone-B	Mean	Red Velox	Golden Clone-B	Mean	Red Velox	Golden Clone-B	Mean
G0: Control	36.27	38.57	37.42	34.27	36.57	35.42	35.23	37.57	36.42
G1: GA_{4+7}+ 6-BA @ 5.5 ppm	39.21	41.51	40.36	37.21	39.51	38.36	38.21	40.51	39.36
G2: GA_{4+7} + 6-BA @ 11 ppm	42.61	44.91	43.76	40.61	42.91	41.76	41.61	43.91	42.76
G3: GA_{4+7} + 6-BA @ 21 ppm	44.17	46.47	45.32	42.17	44.47	43.32	43.17	45.47	44.32
G4: Chlorogenic acid @ 88.5ppm	37.79	40.09	38.94	35.79	38.09	36.94	36.79	39.09	37.94
G5: Chlorogenic acid @ 177 ppm	44.44	46.74	45.59	42.44	44.74	43.59	43.44	45.74	44.59
G6: Chlorogenic acid @ 354 ppm	36.64	38.99	37.75	34.64	36.91	35.75	35.61	37.91	36.75
G7: GA_3 + 6-BA @ 5.5 ppm	38.57	40.86	39.65	36.52	38.82	37.65	37.52	39.84	38.65
G8: GA_3 + 6-BA @ 11 ppm	40.88	43.12	41.95	38.83	41.10	39.95	39.80	42.10	40.95
G9: GA_3 + 6-BA @ 21 ppm	43.49	45.70	44.55	41.45	43.75	42.55	42.42	44.70	43.55
Mean	40.38	42.68		38.38	40.68		39.38	41.68	
C.D.($\leq$ 0.05)									
Russet management chemicals (G)	0.109			0.103			0.0107		
Varieties (V)	0.047			0.056			0.059		
G x V	NS			NS			0.059		

Table 18: Effect of various russet management PGRs on total antioxidant activity (%) (20 days before harvest) of apple cvs. Red Velox and Golden Clone-B

Varieties \ Treatments	2022			2023			Pooled		
	Red Velox	Golden Clone-B	Mean	Red Velox	Golden Clone-B	Mean	Red Velox	Golden Clone-B	Mean
G0: Control	57.03	59.23	58.13	52.94	55.13	54.03	54.98	57.18	56.08
G1: GA_{4+7}+ 6-BA @ 5.5 ppm	63.46	65.66	64.56	59.36	61.56	60.46	61.41	63.61	62.51
G2: GA_{4+7} + 6-BA @ 11 ppm	71.48	73.68	75.28	67.38	69.58	68.48	69.43	71.63	70.53
G3: GA_{4+7} + 6-BA @ 21 ppm	77.82	80.02	78.92	73.72	75.92	74.82	75.77	77.97	76.87
G4: Chlorogenic acid @ 88.5ppm	58.46	60.66	59.56	54.36	56.56	55.46	56.41	58.61	57.51
G5: Chlorogenic acid @ 177 ppm	78.12	80.32	79.22	74.02	76.29	75.12	76.07	78.27	77.17
G6: Chlorogenic acid @ 354 ppm	57.13	59.33	58.23	53.03	55.23	54.13	55.08	57.28	56.18
G7: GA_3 + 6-BA @ 5.5 ppm	60.42	62.62	61.52	56.32	58.52	57.42	58.37	60.57	59.47
G8: GA_3 + 6-BA @ 11 ppm	68.44	70.64	69.54	64.34	66.54	65.44	66.39	68.59	67.49
G9: GA_3 + 6-BA @ 21 ppm	74.56	76.76	75.66	70.46	72.66	71.56	72.51	74.71	73.61
Mean	66.99	68.89		62.59	64.79		64.64	66.84	
C.D.($\leq$ 0.05)									
Russet management chemicals (G)	0.032			0.037			0.062		
Varieties (V)	0.014			0.017			0.028		
G x V	0.048			0.052			0.087		

Table 19: Effect of various russet management PGRs on total antioxidant activity (%) (at harvest) of apple cvs. Red Velox and Golden Clone-B

Varieties \ Treatments	2022			2023			Pooled		
	Red Velox	Golden Clone-B	Mean	Red Velox	Golden Clone-B	Mean	Red Velox	Golden Clone-B	Mean
G0: Control	55.83	59.93	58.83	53.64	55.83	54.73	55.68	57.88	56.78
G1: GA_{4+7}+ 6-BA @ 5.5 ppm	62.26	66.36	65.26	60.16	62.26	61.21	62.11	64.31	63.21
G2: GA_{4+7} + 6-BA @ 11 ppm	70.28	74.38	73.28	68.08	70.28	69.18	70.13	72.39	71.23
G3: GA_{4+7} + 6-BA @ 21 ppm	76.62	80.72	79.62	74.42	76.62	75.52	76.47	78.67	77.57
G4: Chlorogenic acid @ 88.5ppm	57.26	61.36	60.26	55.06	57.26	56.16	57.11	59.31	58.21
G5: Chlorogenic acid @ 177 ppm	76.92	81.02	79.92	74.72	76.92	75.82	76.77	78.97	77.87
G6: Chlorogenic acid @ 354 ppm	55.93	60.03	58.93	53.74	55.93	54.84	55.78	57.98	56.88
G7: GA_3 + 6-BA @ 5.5 ppm	59.22	63.32	62.22	57.02	59.22	58.12	59.07	61.27	60.17
G8: GA_3 + 6-BA @ 11 ppm	67.24	71.34	70.24	65.08	67.24	66.16	67.09	69.29	68.19
G9: GA_3 + 6-BA @ 21 ppm	73.36	77.46	76.36	71.17	73.36	72.27	73.21	75.41	74.31
Mean	65.49	69.59		63.31	65.49		65.34	67.54	
C.D.(≤ 0.05)									
Russet management chemicals (G)	0.072			0.010			0.036		
Varieties (V)	0.032			0.004			0.016		
G x V	0.102			0.014			0.051		

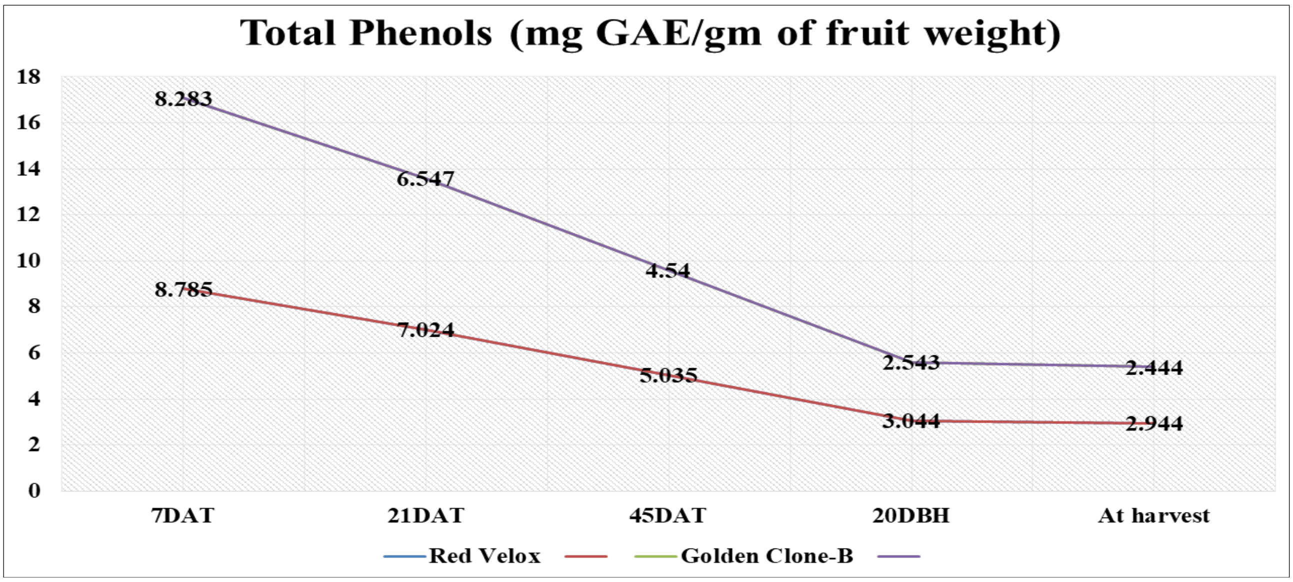

Fig 1: Trend depicted by total phenols (mg GAE/gm of fruit weight) (at different stages after treatment) in two apple cvs. Red Velox and Golden Clone-B

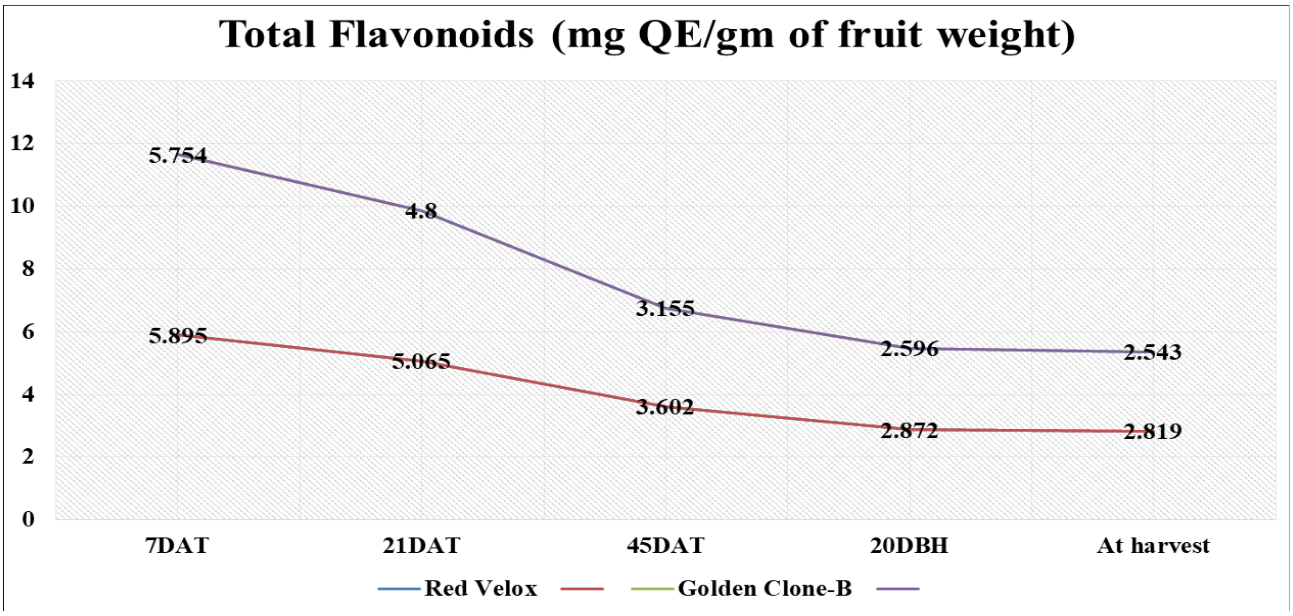

Fig 2: Trend depicted by total flavonoids (mg QE/gm of fruit weight) (at different stages after treatment) in two apple cvs. Red Velox and Golden Clone-B

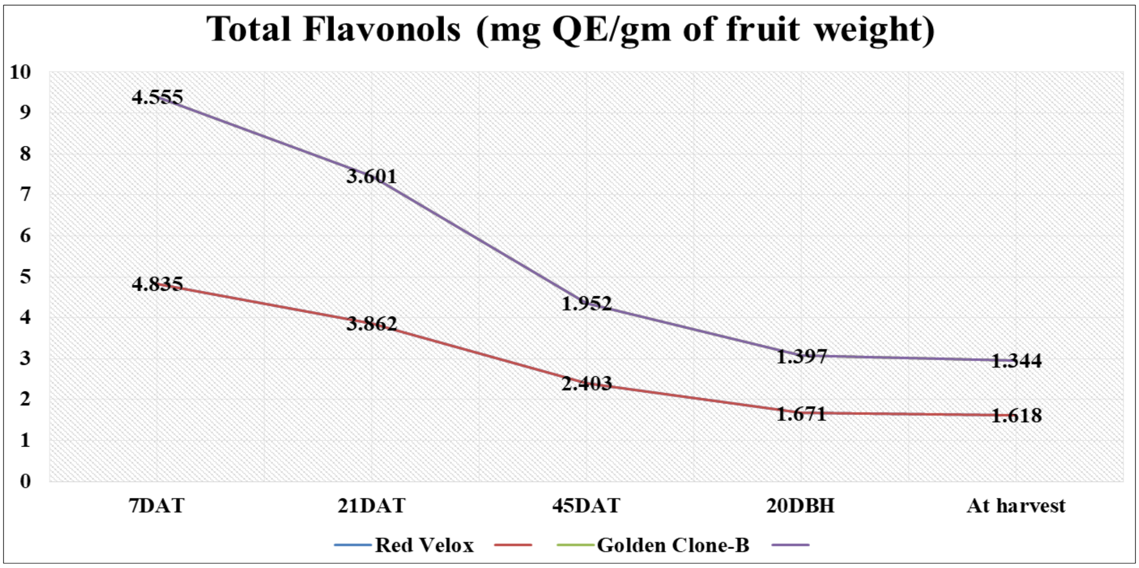

Fig 3: Trend depicted by total flavonols (mg QE/gm of fruit weight) (at different stages after treatment) in two apple cvs. Red Velox and Golden Clone-B

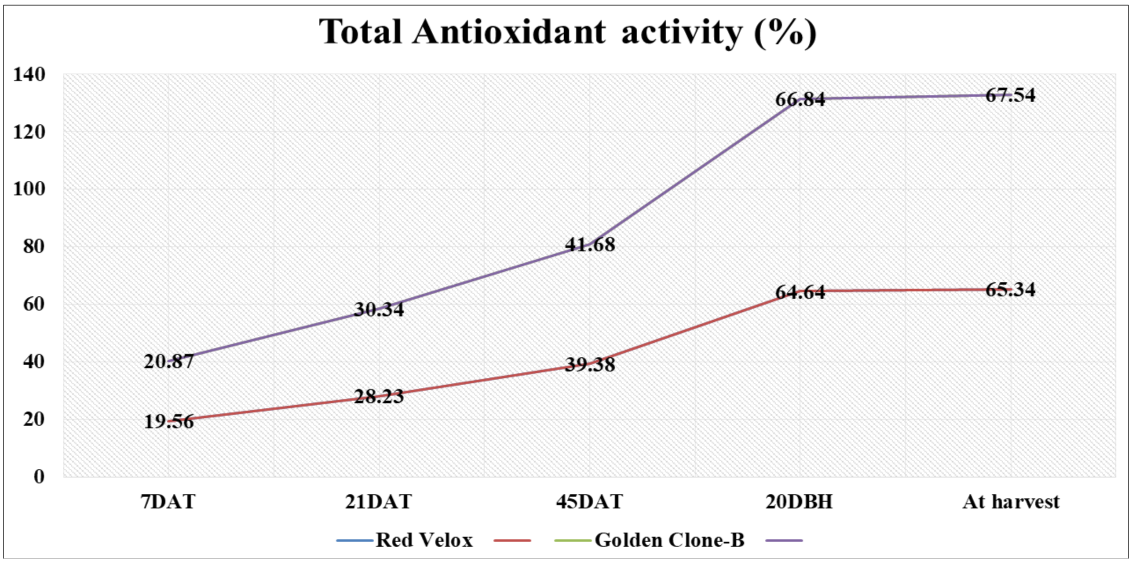

Fig 4: Trend depicted by total antioxidant activity (%) (at different stages after treatment) in two apple cvs. Red Velox and Golden Clone-B

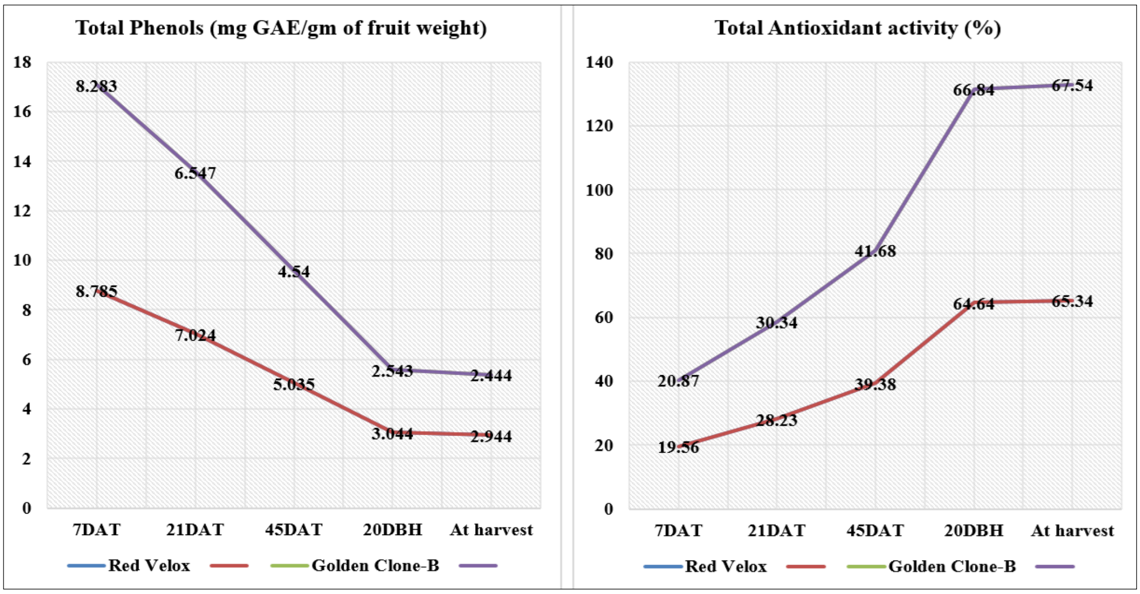

Fig 5: Comparison of the trend depicted by total phenols and total antioxidant activity (%) (at different stages after treatment) in two apple cvs. Red Velox and Golden Clone-B

4. Discussion

The present investigation provides a comprehensive biochemical interpretation of apple fruit russeting by integrating stage-wise changes in phenolic metabolism, flavonoid and flavonol dynamics, and antioxidant activity under different russet management treatments. By focusing exclusively on the biochemical component of the study, the discussion establishes a mechanistic link between early developmental metabolic events in the fruit peel and the final expression of russeting at harvest. The findings clearly demonstrate that russeting is not merely a superficial morphological defect but a developmentally regulated biochemical disorder governed by the balance between phenylpropanoid activation and oxidative homeostasis.

4.1 Russeting as a developmentally regulated biochemical disorder

Traditionally, russeting has been described primarily in terms of its visible symptoms on the fruit surface. However, the biochemical data generated in the present study unequivocally show that russeting is initiated at a much earlier developmental stage, well before visible symptoms appear. The consistently high levels of phenolic compounds, flavonoids and flavonols recorded during the first few weeks after treatment indicate that early fruit development represents a critical window during which metabolic perturbations determine russet susceptibility.

During this period, rapid epidermal cell expansion occurs concurrently with cuticle formation. Any imbalance between fruit growth rate and cuticle deposition can impose mechanical stress on the epidermis, triggering wound-like biochemical responses. The elevated phenylpropanoid activity observed at early stages can therefore be interpreted as a physiological response to epidermal stress. When this response exceeds a threshold, it predisposes the fruit surface to cuticular microcracking and subsequent periderm formation, ultimately manifesting as russeting.

4.2 Phenolic metabolism and its role in russet initiation

Total phenolic content emerged as a central biochemical determinant of russet development. Across both cultivars and all treatments, phenolic concentration was highest at 7 and 21 days after treatment and declined progressively toward harvest. This pattern strongly suggests that phenylpropanoid metabolism is most active during early fruit development, coinciding with the period of greatest epidermal vulnerability.

Treatments involving chlorogenic acid, particularly at higher concentrations, consistently enhanced phenolic accumulation during early stages. Chlorogenic acid is a key intermediate of the phenylpropanoid pathway, and its exogenous application likely amplified endogenous metabolic flux, resulting in elevated phenolic pools. While such accumulation may contribute to short-term stress protection, excessive phenolic synthesis appears to accelerate suberization-related processes, thereby increasing russet severity.

In contrast, GA_{4+7} + 6-BA treatments moderated early phenolic accumulation. Gibberellins are known to promote cell expansion and cuticle development, while cytokinins influence cell division and metabolic balance. Their combined application may have synchronized epidermal growth with cuticle deposition, reducing mechanical stress and diminishing the need for excessive phenylpropanoid activation.

4.3 Decline in phenolic concentration toward harvest: metabolic reallocation

The progressive decline in measured phenolic content from mid-development to harvest does not necessarily indicate reduced phenylpropanoid activity but rather reflects metabolic reallocation. As fruit growth accelerates, dilution effects due to increasing fresh weight contribute to lower phenolic concentrations on a fresh weight basis. Moreover, soluble phenolic compounds synthesized during early development may be converted into insoluble structural polymers such as lignin and suberin, which are integral to periderm tissue.

This interpretation is supported by the negative correlation observed between phenolic content and antioxidant activity at harvest. Phenolics persisting in russet-prone fruits at maturity appear to be structurally bound rather than functionally active as antioxidants. Thus, the apparent decline in phenolic concentration represents a shift from soluble defensive metabolites toward structural reinforcement of the peel.

4.4 Flavonoids and epidermal stress modulation

Flavonoids followed a developmental trajectory similar to total phenols, with maximum concentrations at early stages and a steady decline toward harvest. Flavonoids serve multiple physiological roles, including UV protection, antioxidative defense and modulation of cellular signaling pathways. Their early accumulation likely reflects heightened epidermal sensitivity to environmental stress factors during initial fruit growth.

However, excessive flavonoid accumulation may reduce cuticular flexibility by increasing cell wall rigidity, thereby exacerbating susceptibility to microcracking. The consistently lower flavonoid levels observed under GA_{4+7} + 6-BA treatments suggest that these growth regulators mitigated epidermal stress by promoting balanced growth, reducing the need for enhanced flavonoid synthesis.

The negative relationship between flavonoid content and antioxidant activity at harvest further indicates that flavonoids in russeted fruits are primarily associated with structural modification rather than oxidative defense at later stages of development.

4.5 Flavonols as sensitive indicators of early russet susceptibility

Among the phenolic subclasses examined, flavonols exhibited the most pronounced sensitivity to developmental stage and treatment. Their high concentration during early fruit development, particularly under chlorogenic acid treatments, suggests that flavonols may serve as early biochemical indicators of russet susceptibility.

Flavonols are often synthesized in response to stress-induced activation of the phenylpropanoid pathway. The sharp decline in flavonol content toward harvest likely reflects their incorporation into downstream products associated with suberization and periderm formation. The strong negative correlation between flavonol concentration and antioxidant activity at harvest supports this functional transition.

4.6 Antioxidant activity and metabolic transition during fruit maturation

In contrast to phenolic compounds, total antioxidant activity increased progressively from early fruit development to harvest. This inverse relationship highlights a metabolic transition from structural reinforcement toward oxidative balance as fruit maturation advances.

During early development, metabolic resources appear to be preferentially allocated toward phenylpropanoid synthesis and peel reinforcement. As the fruit approaches maturity, increased respiratory activity and reactive oxygen species production necessitate enhanced antioxidant defenses. Treatments that moderated early phenolic accumulation were associated with higher antioxidant activity at harvest, suggesting that balanced early metabolism enables more effective oxidative regulation later in development.

4.7 Cultivar-specific biochemical responses

Distinct cultivar-specific differences were evident throughout the study. Red Velox consistently exhibited higher concentrations of phenolic compounds, flavonoids and flavonols, whereas Golden Clone-B generally showed higher antioxidant activity at later stages. These differences likely arise from inherent variation in epidermal structure, cuticle composition and metabolic regulation between cultivars.

Such variation underscores the importance of tailoring russet management strategies to cultivar-specific physiological characteristics rather than adopting a uniform approach across genotypes.

4.8 Integrated interpretation of treatment effects

The collective analysis of biochemical parameters indicates that russet management chemicals exert their effects primarily by modulating early-stage phenylpropanoid metabolism. GA_{4+7} + 6-BA treatments effectively synchronized epidermal expansion with cuticle development, thereby reducing biochemical conditions conducive to russet initiation. In contrast, higher concentrations of chlorogenic acid intensified early phenolic synthesis, promoting suberization-related processes and increasing russet severity.

These findings emphasize that successful russet management depends on precise regulation of metabolic flux during critical developmental windows rather than indiscriminate suppression of phenolic metabolism.

4.9 Conceptual biochemical model of russet development

Based on the present findings, russet development in apple can be conceptualized as a three-phase biochemical process: (i) an initiation phase characterized by elevated phenylpropanoid activity and accumulation of phenols, flavonoids and flavonols during early fruit development; (ii) a transition phase involving conversion of soluble phenolics into structural polymers; and (iii) a maturation phase dominated by enhanced antioxidant activity and oxidative balance regulation. The extent of russet expression at harvest is largely determined by metabolic events occurring during the initiation phase.

4.10 Implications for russet management and future research

The present study establishes a robust biochemical framework for understanding russet development in apple. Identification of early-stage biochemical markers, particularly flavonols, offers potential for predictive assessment of russet risk. Future research should focus on integrating biochemical indicators with physiological and molecular approaches to refine russet management strategies and improve fruit surface quality.

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