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Study of association, direct and indirect effects of mineral nutrients in wood apple (*Limonia acidissima* L.) genotypes across agro-climatic zones of Karnataka

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Abstract

Background: Wood apple (*Limonia acidissima* L.), a drought-tolerant underutilized fruit tree, is rich in mineral nutrients essential for human nutrition and plant physiology. Despite its agronomic and nutraceutical significance, systematic studies quantifying the interrelationships among macro- and micronutrients across diverse agro-climatic zones remain scarce. This study aimed to evaluate the correlation coefficients and path coefficients (direct and indirect effects) among nine mineral nutrients Fe, Mn, Zn, Cu, P, K, Ca, Mg and S in wood apple genotypes collected from 11 districts of Karnataka, India. A reconnaissance survey across five agro-climatic zones of Karnataka identified diverse wood apple genotypes aged 10-50 years. Mineral nutrient concentrations (Fe, Mn, Zn, Cu, P, K, Ca, Mg and S) were estimated using standard wet digestion and analytical methods. Pearson's correlation and path coefficient analyses were performed using R statistical software. Significant positive correlations were observed between Fe and S ($r = 0.522^{**}$) and between Mn and Ca ($r = 0.51^{**}$). Path analysis revealed Fe (0.802) as having the highest direct positive effect on S, followed by Ca (0.290) and Zn (0.334). K exhibited a strong negative direct effect (-0.520). The study highlights critical nutrient associations in wood apple, providing a foundation for targeted breeding, soil management and nutritional enhancement strategies.

Keywords: *Limonia acidissima*, mineral nutrients, correlation analysis, path coefficient analysis, Karnataka, agro-climatic zones, underutilized fruit crops

1. Introduction

Limonia acidissima L. (syn. *Feronia limonia*, *Feronia elephantum*), commonly known as wood apple, elephant apple, or curd fruit, belongs to the family Rutaceae. It is a slow-growing, drought-resistant tree indigenous to dry deciduous forests of the Indian subcontinent, Sri Lanka, Myanmar and parts of Southeast Asia (Sharma *et al.*, 2015) [28]. In India, the tree is widely distributed in Karnataka, Tamil Nadu andhra Pradesh and the semi-arid tracts of Maharashtra.

Wood apple fruit possesses a hard, woody outer shell encasing a sticky, aromatic pulp with a complex nutritional matrix that includes carbohydrates, proteins, dietary fibre, ascorbic acid, beta-carotene, riboflavin, thiamine and a rich array of mineral nutrients (Maity *et al.*, 2019; Patel *et al.*, 2017) [19, 22]. The mineral constituents—iron (Fe), manganese (Mn), zinc (Zn), copper (Cu), phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg) and sulphur (S)—play multifaceted roles in both plant metabolism and human nutrition (Marschner, 2012) [20]. In plants, these nutrients regulate enzymatic activity, photosynthesis, osmotic balance, structural integrity of cell walls and signalling cascades (Hawkesford *et al.*, 2012) [11].

Despite the nutraceutical and agroforestry value of wood apple, the species remains taxonomically and agronomically undercharacterized and its genetic diversity remains poorly understood (Lim, 2012) [17]. Karnataka, with its diverse agro-climatic zones ranging from arid northern tracts to humid hill regions, harbours considerable phenotypic variation in wood apple populations. Understanding the inter-relationships among mineral nutrients across these zones is critical for the development of nutritionally superior genotypes through selection and breeding, as well as for designing zone-specific soil and foliar nutrition programmes.

Correlation analysis quantifies the degree and direction of association between pairs of variables, while path coefficient analysis, introduced by Wright (1921) [32] and later applied to plant breeding by Dewey and Lu (1959) [8], partitions the observed correlation coefficient into direct and indirect effects. This dual analytical approach enables researchers to discern which nutrients exert genuine independent influence on a target mineral versus which appear correlated merely through their association with a third variable (Singh and Chaudhary, 1985) [29]. Such insights are particularly valuable in nutritional breeding programmes, facilitating precise selection criteria.

The present investigation was undertaken with the following objectives: (i) to characterize the mineral nutrient composition (Fe, Mn, Zn, Cu, P, K, Ca, Mg and S) in diverse wood apple genotypes collected from 11 districts spanning five agro-climatic zones of Karnataka; (ii) to assess the pairwise correlations among the mineral nutrients; and (iii) to partition the genotypic correlations into direct and indirect path coefficients, with sulphur as the dependent variable of interest.

2. Materials and Methods

2.1 Survey Area and Genotype Selection

A systematic reconnaissance survey was conducted across 11 districts of Karnataka to identify and document diverse wood apple genotypes. The districts covered were Bagalkot, Dharwad, Koppal, Hassan, Belagavi, Ballari, Chitradurga, Chikmagalur, Raichur, Tumkur and Bengaluru Rural. These districts span five distinct agro-climatic zones of Karnataka as defined by the Karnataka State Department of Agriculture (2018): Northern Dry Zone (Zone III), Central Dry Zone (Zone IV), Southern Transition Zone (Zone VII), Northern Transition Zone (Zone VIII) and the Hilly Zone (Zone IX), thus representing the full spectrum of edaphic and climatic diversity in the state.

Genotype selection during the survey was governed by pre-defined, reproducible criteria following the protocols of Chadha and Pareek (1994) [6] for underutilized fruit crop surveys:

1. Tree age was restricted to 10-50 years, since this ontogenetic window corresponds to the period of maximum reproductive output and physiological maturity in wood apple (Patel *et al.*, 2017) [22].
2. Trees exhibiting visible morphological diversity in fruit size, shape, pulp colour, aroma and canopy architecture were preferentially selected to maximise genetic representativeness.
3. To minimise sampling bias due to microenvironmental clustering, a minimum inter-tree distance of 500 m was maintained when multiple trees were sampled from the same locality (Rao *et al.*, 2010) [25].
4. Trees showing symptoms of severe biotic or abiotic stress were excluded.

In total, 36 wood apple genotypes were identified and documented with GPS coordinates, local vernacular names and photographic records. Each genotype was assigned a unique accession code for subsequent analysis.

2.2 Collection of Fruit Samples

Mature, fully ripened wood apple fruits were harvested from each selected genotype at the physiological maturity stage, characterised by a hard, greyish-brown shell and fragrant,

sticky pulp, as described by Bose *et al.* (2003) [2]. Five fruits per tree were collected from three spatially distinct branches (upper, middle and lower canopy) to account for within-tree variation. Fruits were harvested during the months of January to March, coinciding with the peak fruiting season across all survey locations. Samples were transported in insulated containers to the laboratory within 24 hours of collection and processed immediately.

2.3 Sample Preparation and Digestion

The pulp from the five fruits per genotype was pooled, homogenised using a mortar and pestle and a representative sub-sample of approximately 10 g fresh weight was taken. Samples were oven-dried at 65 ± 2 °C to constant weight (48-72 hours) and ground to a fine powder using a stainless-steel Wiley mill fitted with a 0.5-mm mesh screen. The dried, powdered samples were stored in airtight polyethylene bags at 4 °C until chemical analysis.

Mineral extraction was carried out by tri-acid wet digestion following the procedure of Mahajan and Gupta (2000) [18]. Approximately 0.5 g of the oven-dried plant material was weighed into a 100-mL Kjeldahl flask. A 10-mL aliquot of the nitric-perchloric-sulfuric acid mixture in the ratio 9:3:1 (v/v/v) was added. Digestion was performed on a hot plate at progressively increasing temperatures: 80 °C for 30 minutes, followed by 120 °C for 60 minutes and finally at 200 °C until colourless, fume-free digestate was obtained. The digest was cooled, quantitatively transferred to a 50-mL volumetric flask and made up to volume with double-distilled water (DDW). Reagent blanks and certified reference materials (NIST SRM 1570a, Spinach Leaves) were digested concurrently for quality assurance.

2.4 Mineral Nutrient Analysis

Nine mineral nutrients were determined as follows, following standard analytical protocols (AOAC, 2000; Jackson, 1973) [1, 13]:

2.4.1 Iron (Fe), Manganese (Mn), Zinc (Zn) and Copper (Cu): Micronutrient cations were estimated by Atomic Absorption Spectrophotometry (AAS) using a Perkin-Elmer AAnalyst 400 (Perkin-Elmer, USA) instrument at wavelengths of 248.3, 279.5, 213.9 and 324.7 nm, respectively, with an air-acetylene flame. Calibration curves were prepared using certified multi-element standard solutions (Merck, Germany) at five concentration levels bracketing the expected sample range. Results were expressed as mg per 100 g fresh weight.

2.4.2 Phosphorus (P): Available phosphorus was determined colorimetrically by the vanadomolybdophosphoric acid yellow colour method (Jackson, 1973) [13] using a UV-visible spectrophotometer (Shimadzu UV-1800) at 430 nm. A standard curve was prepared from potassium dihydrogen phosphate (KH_2PO_4).

2.4.3 Potassium (K): Potassium was measured by flame photometry (Elico CL 378, India) using a potassium hollow-cathode lamp. Standards were prepared from analytical-grade KCl. Readings were taken at 766.5 nm.

2.4.4 Calcium (Ca) and Magnesium (Mg): Ca and Mg were determined by EDTA titration (complexometric method) following the procedure of Ranganna (1986) [24].

Briefly, the digest was buffered at pH 10 using ammonium chloride-ammonium hydroxide buffer; Eriochrome Black T (EBT) was used as indicator for Mg and murexide for Ca. Results were calculated from the titration volumes and expressed as mg per 100 g fresh weight.

2.4.5 Sulphur (S): Total sulphur content was estimated turbidimetrically by precipitation as barium sulphate (BaSO_4) following the method of Chesnin and Yien (1951)^[7]. The turbidity was read at 420 nm on a UV-visible spectrophotometer. A standard curve was prepared using potassium sulphate (K_2SO_4). All determinations were performed in triplicate and mean values were used for statistical analysis.

2.5 Statistical Analysis

All data were subjected to analysis using R statistical software version 4.2.2 (R Core Team, 2022). Descriptive statistics—mean, standard deviation and coefficient of variation—were computed for all nine mineral nutrients. Pairwise Pearson's genotypic correlation coefficients (r) were estimated according to the procedure outlined by Singh and Chaudhary (1985)^[29]. Significance of correlation coefficients was tested at the 5% ($r = 0.05^*$) and 1% ($r = 0.01^{**}$) probability levels using the two-tailed t-test with $n - 2$ degrees of freedom, where $n = 36$ genotypes.

Path coefficient analysis was performed following the methodology of Dewey and Lu (1959)^[8] as adapted for mineral nutrient studies by Kumar *et al.* (2013)^[14]. Sulphur (S) was designated as the dependent (response) variable, given its biological significance as a structural constituent of amino acids (methionine and cysteine), vitamins (biotin and thiamine), coenzymes (coenzyme A) and its pivotal role in plant defence mechanisms (Hawkesford *et al.*, 2012)^[11]. The path coefficient equation system was solved as $\mathbf{P} = \mathbf{R}^{-1}\mathbf{C}$, where $\mathbf{P}$ is the vector of direct path coefficients, $\mathbf{R}$ is the correlation matrix of independent variables and $\mathbf{C}$ is the vector of correlations between the independent variables and the dependent variable. Residual effects were calculated as 1

– $\sum p_i r_i Y$, where p_i is the direct path coefficient and $r_i Y$ is the correlation coefficient of the i -th variable with the dependent variable. All analyses were conducted at the 5% and 1% levels of significance.

3. Results & Discussion

3.1 Correlation Analysis Among Mineral Nutrients

Pearson's genotypic correlation coefficients among nine mineral nutrients in wood apple genotypes are presented in Table 1. Among the 36 pairwise correlations computed, two were statistically significant at the 1% level of probability ($p < 0.01$), indicating highly specific and reproducible associations despite the broad genetic and environmental diversity of the sampled genotypes.

The most prominent significant positive correlation was observed between Fe and S ($r = 0.522^{**}$). This association suggests a coupled metabolic relationship wherein iron—an essential cofactor for sulphate reduction enzymes, particularly adenosine 5'-phosphosulphate reductase (APR) and sulphite reductase—promotes the efficient assimilation of sulphur in plant tissues (Saito, 2004)^[27]. Concurrently, a strong positive correlation was observed between Mn and Ca ($r = 0.51^{**}$), which is consistent with the co-operative roles of these elements in cell wall pectin cross-linking and Ca^{2+} -dependent enzymatic processes that require Mn as a redox co-factor (White and Broadly, 2003)^[31].

Several non-significant but directionally consistent trends were noted. Mn showed positive correlations with P ($r = 0.322$), K ($r = 0.29$) and S ($r = 0.374$), while Ca also showed a positive trend with P ($r = 0.339$) and S ($r = 0.271$). Conversely, Fe and Ca exhibited a negative association ($r = -0.327$), a relationship well documented in the literature and attributed to the antagonism between these ions during root uptake, mediated by competition at IRT1 (Iron-regulated Transporter 1) and other divalent cation transporters (Brumbarova *et al.*, 2015)^[4]. K and Ca also showed a negative association ($r = -0.267$), reflecting the classical ionic antagonism between monovalent and divalent cations in soil solution and at root surfaces.

Table 1: Pearson's genotypic correlation matrix for mineral nutrients (mg/100 g) in wood apple genotypes ($n = 36$). ****** significant at $p < 0.01$.

Mineral	Fe (mg/100 g)	Mn (mg/100 g)	Zn (mg/100 g)	Cu (mg/100 g)	P (mg/100 g)	K (mg/100 g)	Ca (mg/100 g)	Mg (mg/100 g)	S (mg/100 g)
Fe (mg/100 g)	1	0.098	−0.115	0.092	0.191	0.211	−0.327	−0.272	0.522**
Mn (mg/100 g)		1	0.162	0.032	0.322	0.29	0.51**	−0.204	0.374
Zn (mg/100 g)			1	0.323	−0.027	0.176	0.058	0.158	0.142
Cu (mg/100 g)				1	−0.234	−0.219	0.089	−0.085	0.15
P (mg/100 g)					1	0.003	0.339	−0.246	0.29
K (mg/100 g)						1	−0.267	0.242	−0.172
Ca (mg/100 g)							1	−0.078	0.271
Mg (mg/100 g)								1	−0.239
S (mg/100 g)									1

Values in red with ****** are significant at the 1% probability level.

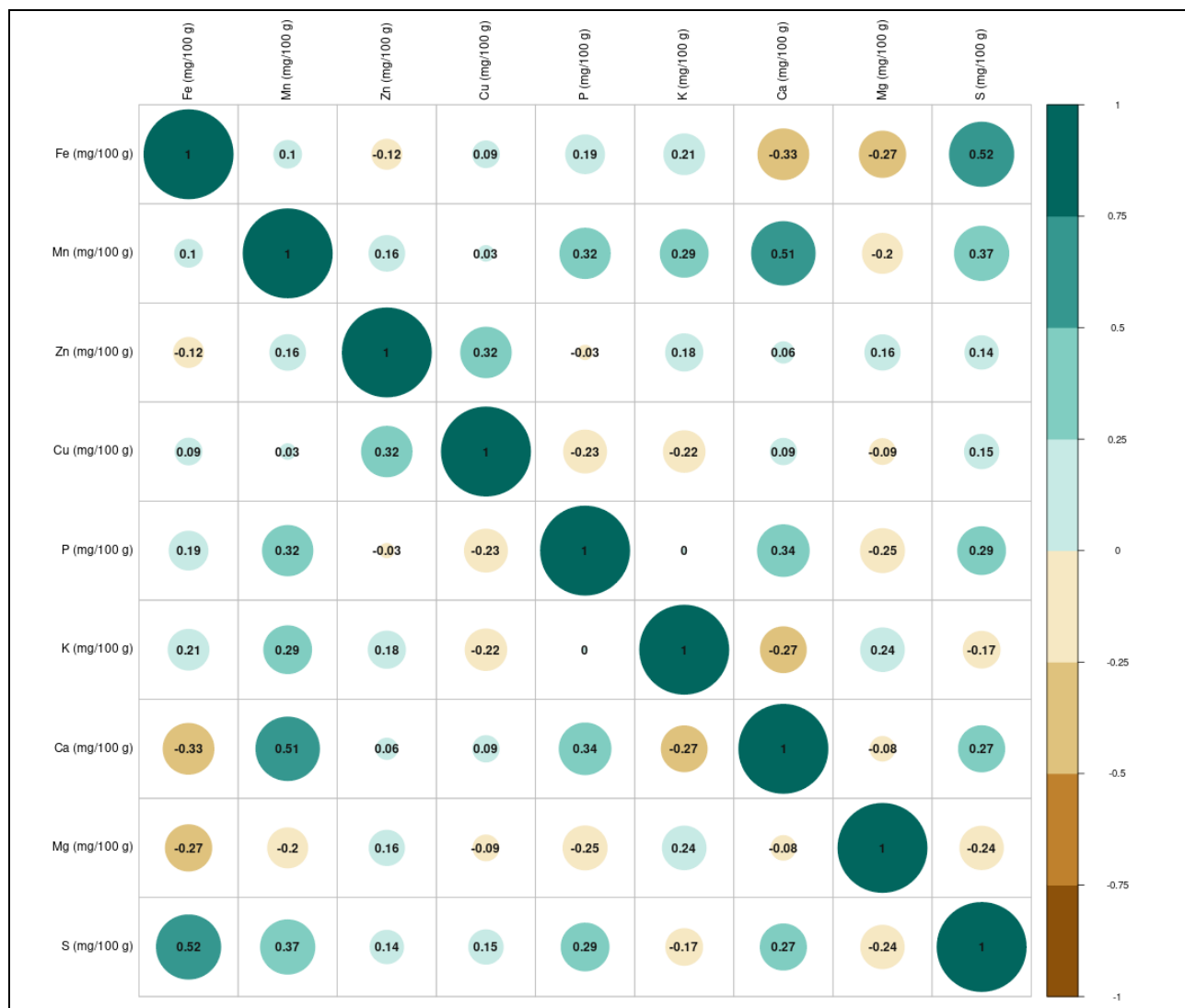


Fig 1: Correlogram diagram of the different mineral nutrients

3.2 Path Coefficient Analysis Direct and Indirect Effects on Sulphur

The direct and indirect path coefficients of eight causal mineral nutrients on sulphur (S) content, along with their genotypic correlations with S, are presented in Table 2. The residual effect of the path analysis was 0.143, indicating that approximately 85.7% of the total variation in sulphur content was accounted for by the eight nutrients included in the model, validating the adequacy of the chosen causal variables (Singh and Chaudhary, 1985) [29].

3.2.1 Iron (Fe): Fe exhibited the highest direct positive path coefficient on S (0.802), substantially exceeding its genotypic correlation with S ($r = 0.527$), indicating that Fe is a principal and autonomous driver of sulphur accumulation in wood apple pulp. The biological basis for this lies in the iron-sulphur (Fe-S) cluster assembly pathway, which is fundamental to electron transfer chains in mitochondria and chloroplasts (Lill, 2009) [15]. Indirect effects of Fe through other nutrients were generally minor and negative (via Ca: -0.089 ; via Mg: -0.027), slightly attenuating but not obscuring the strong direct effect.

3.2.2 Zinc (Zn): Zn recorded a direct path coefficient of 0.334 on S, with a relatively modest genotypic correlation ($r = 0.158$). This positive direct effect likely reflects the

requirement for zinc in the synthesis of cysteine-rich metallothionein and phytochelatin proteins, which contain sulphur-bearing thiol groups (Rauser, 1999) [26]. Indirect effects were minimal (via Fe: -0.076 ; via Cu: -0.073).

3.2.3 Calcium (Ca): Ca contributed a direct path coefficient of 0.290 with a genotypic correlation of 0.284 with S, making its direct and total effects nearly concordant—an indication that Ca's influence on S is largely independent of other nutrients. Calcium is known to indirectly regulate sulphur metabolism through its role as a second messenger in signal transduction cascades that activate sulphate transporter gene expression (Buchner *et al.*, 2004) [5].

3.2.4 Magnesium (Mg): Mg showed a small positive direct effect on S (0.107) but a negative genotypic correlation (-0.228), indicating substantial masking through negative indirect pathways, particularly via Fe (-0.205) and K (-0.156). This suppression effect is ecologically plausible: high Mg may indirectly depress S through competitive inhibition with K at root transporters, which in turn reduces sulphate influx.

3.2.5 Potassium (K): K demonstrated the strongest negative direct path coefficient (-0.520) on S, with a negative genotypic correlation (-0.155). K and S are both highly

mobile anions/cations in the phloem and compete for transport loading in vascular tissues. Elevated K concentrations may also lower the electrochemical gradient that drives sulphate uptake through H^+/SO_4^{2-} co-transporters (Marschner, 2012)^[20].

3.2.6 Copper (Cu): Cu showed a negative direct effect (−0.194) on S with a negligible genotypic correlation (0.161). Cu is a well-documented antagonist of Fe in root uptake pathways and may indirectly affect sulphur via iron-sulphur cluster disruption at high concentrations (Hall, 2002). The residual positive correlation despite a negative direct effect is attributable to positive indirect effects through Zn (0.125) and K (0.088).

3.2.7 Phosphorus (P): P showed a small negative direct

effect (−0.065) on S, with a positive genotypic correlation ($r = 0.299$). The discrepancy indicates that most of P's positive association with S operates through indirect pathways, especially via Fe (0.163) and Ca (0.108), highlighting the importance of the Fe-P-S metabolic network in woody fruit tissues (Hell and Hillebrand, 2001)^[12].

3.2.8 Manganese (Mn): Mn showed a moderate positive direct effect (0.292) on S and a positive genotypic correlation (0.375). As a cofactor for sulphate reductase and several antioxidant enzymes (e.g., Mn-superoxide dismutase), Mn can facilitate sulphur assimilation and reduce oxidative decomposition of S-containing amino acids (Ducic and Polle, 2005)^[9]. The strong indirect effect of Mn through Ca (0.149) further augments its overall association with S.

Table 2: Direct and indirect path coefficients of mineral nutrients (causal variables) on sulphur (S) content (dependent variable) in wood apple genotypes. Diagonal values (bold) represent direct effects; off-diagonal values represent indirect effects mediated through the respective column variable. Residual effect = 0.143.

Nutrient	Fe	Mn	Zn	Cu	P	K	Ca	Mg	Gen. Corr. with S
Fe	0.802	0.029	−0.032	−0.021	−0.013	−0.123	−0.089	−0.027	0.527
Mn	0.080	0.292	0.056	−0.007	−0.021	−0.154	0.149	−0.021	0.375
Zn	−0.076	0.049	0.334	−0.073	−0.001	−0.133	0.034	0.023	0.158
Cu	0.086	0.010	0.125	−0.194	0.014	0.088	0.037	−0.006	0.161
P	0.163	0.095	0.004	0.041	−0.065	−0.024	0.108	−0.023	0.299
K	0.189	0.087	0.085	0.033	−0.003	−0.520	−0.058	0.032	−0.155
Ca	−0.248	0.151	0.040	−0.025	−0.024	0.104	0.290	−0.004	0.284
Mg	−0.205	−0.058	0.070	0.010	0.014	−0.156	−0.010	0.107	−0.228

Bold diagonal values indicate direct path coefficients. Residual = 0.143; $R^2 = 0.857$.

The results of the present study provide a comprehensive understanding of the inter-relationships among mineral nutrients in wood apple genotypes from Karnataka's diverse agro-climatic zones. The significant positive Fe-S correlation ($r = 0.522^{**}$) and the highest direct path coefficient of Fe on S (0.802) are consistent with the established biochemistry of iron-sulphur (Fe-S) cluster proteins, which include ferredoxins, Rieske proteins and aconitase, all of which require both Fe and S for their catalytic function (Lill and Mühlenhoff, 2008)^[16]. These results corroborate the findings of Marschner (2012)^[20] and Saito (2004)^[27], who demonstrated that sulphur deficiency impairs Fe-S cluster assembly and that Fe availability modulates the expression of sulphate transporter genes.

The significant Mn-Ca correlation ($r = 0.51^{**}$) is in agreement with White and Broadly (2003) and Welch and Graham (2004)^[30], who documented co-regulation of these elements in the apoplast and cell wall matrix. In wood apple, the extraordinarily thick and lignified pericarp and the dense fibrous pulp matrix may provide an expanded apoplastic compartment for Ca-Mn co-deposition, amplifying this association relative to soft-fleshed fruits.

The negative direct effect of K on S (−0.520) corroborates the ionic antagonism between K^+ and SO_4^{2-} in phloem loading, as described by Broadley *et al.* (2012). High potassium concentrations are known to hyperpolarise root cell membranes, potentially reducing the electromotive force driving sulphate uptake by high-affinity sulphate transporters of the SULTR family (Hawkesford *et al.*, 2012)^[11]. The practical implication for wood apple cultivation is that potassium fertilisation programmes in K-deficient agro-climatic zones should be complemented by sulphur supplementation to prevent nutritional antagonism.

The high residual effect value of 0.143 ($R^2 = 0.857$) indicates that the eight mineral nutrients together explain approximately 85.7% of sulphur variation, suggesting that the model is well specified. The remaining unexplained variation (~14.3%) may be attributed to genetic factors (e.g., variation in SULTR transporter genes), rootzone microbiome-mediated sulphur mineralisation differences across agro-climatic zones, or other unmeasured variables such as organic sulphur compounds (glucosinolates, alliin) that contribute to total sulphur estimates (Saito, 2004)^[27].

These findings are broadly consistent with correlation and path studies conducted in other fruit crops. Kumar *et al.* (2013)^[14] reported significant positive Fe-S correlations in amla (*Phyllanthus emblica*) genotypes from similar agro-climatic zones, while Pandey *et al.* (2020)^[21] documented analogous Mn-Ca associations in tamarind. The novelty of the present study lies in its application of path analysis to wood apple, a hitherto uncharacterised species in this analytical framework and in the breadth of agro-climatic zones covered.

4. Conclusion

This investigation revealed that iron (Fe) exerts the strongest independent direct effect on sulphur (S) accumulation in wood apple genotypes (direct path coefficient = 0.802), followed by zinc (Zn, 0.334), calcium (Ca, 0.290) and manganese (Mn, 0.292). Potassium (K) demonstrated a strong negative direct effect (−0.520), indicating an antagonistic relationship with sulphur. Two correlation coefficients reached statistical significance at the 1% probability level: Fe-S ($r = 0.522^{**}$) and Mn-Ca ($r = 0.51^{**}$).

From a plant breeding and agronomy perspective, the results suggest that genotypes with high Fe and Mn content are likely to simultaneously possess elevated S and Ca levels, respectively, providing composite selection indices for multi-nutrient improvement. Agronomically, potassium applications in the Northern Dry Zone (Zone III) and Central Dry Zone (Zone IV)—where K deficiency is prevalent—should be paired with sulphur fertilisation to prevent nutrient antagonism and ensure adequate sulphur-containing amino acid synthesis in fruit pulp.

Future research should explore the genetic architecture of Fe-S and Mn-Ca associations through quantitative trait locus (QTL) mapping or genome-wide association studies (GWAS) in *Limonia acidissima* and should assess the stability of these nutrient associations across years and agro-climatic zones through multi-environment trials.

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