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GENETIC AND BREEDING STRATEGIES FOR BIOFORTIFICATION AND NUTRITIONAL ENHANCEMENT IN HORTICULTURAL CROPS

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ABSTRACT

Micronutrient malnutrition continues to be a significant concern worldwide, as a large proportion of the population lacks sufficient quantities of one or more vital micronutrients through their regular diet. Horticultural commodities, particularly vegetables, fruits, roots and tubers, and spices, provide considerable potential for enhancing dietary nutrition and can serve as an important complement to biofortification programs targeting staple food crops. This review explores recent genetic, genomic, and biotechnological strategies employed to improve nutritional quality in horticultural crops. These approaches include conventional breeding, marker-assisted breeding, genomic selection, QTL analysis, genome-wide association studies, integrated multi-omics, and modern genome-editing technologies such as CRISPR/Cas9, CRISPR/Cas12, CRISPR/Cas13, base editing, and prime editing. The review focuses on the genetic and molecular mechanisms involved in the accumulation of major nutritional constituents, including provitamin A carotenoids, ascorbic acid, tocopherols, folates, iron, zinc, selenium, anthocyanins, flavonoids, phenolic compounds, proteins, and dietary fibre. The contribution of transcription factors, hormonal regulation, nutrient transporters, and metabolic pathways to nutrient biosynthesis and accumulation is considered across a wide range of horticultural crops, including tomato, potato, sweet potato, carrot, cassava, banana, citrus, apple, mango, Brassica vegetables, vegetable legumes, and spices. Although substantial advances have been achieved, improving nutritional quality remains complicated by undesirable effects on yield, genotype × environment interactions, fluctuations in trait expression under different growing conditions, and the presence of anti-nutritional compounds that may restrict nutrient availability. The development of precise genome-editing technologies has opened new possibilities for simultaneously modifying several nutritional traits within the same genetic background. Nevertheless, the successful incorporation of these technologies into commercial horticultural production is influenced by regulatory requirements, biosafety considerations, consumer perceptions, and the overall performance of improved cultivars. Future nutritional breeding programs should therefore move beyond single-gene approaches and emphasize the integration of genomics, phenomics, multi-omics, and artificial intelligence-assisted breeding systems. Such integrated strategies can help address the complex genetic architecture of nutritional traits while simultaneously improving trait stability across environments and enhancing the bioavailability of nutrients.

KEYWORDS: biofortification; horticultural crops; genomic selection; CRISPR/Cas gene editing; QTL mapping; micronutrient deficiency; carotenoid biosynthesis; anthocyanin biosynthesis

1. INTRODUCTION

Hidden hunger micronutrient deficiency without visible acute undernutrition persists even where caloric intake is adequate, with iron, zinc, vitamin A, and folate deficiencies most consequential for child development (Weffort & Lamounier, 2023). Horticultural crops are naturally rich in carotenoids, ascorbate, flavonoids, anthocyanins, and glucosinolates, and higher fruit/vegetable intake continues to be associated with reduced mortality (Devirgiliis *et al.,* 2024), yet horticultural biofortification has received far less systematic breeding investment than staple-crop programmes

(Bashir *et al.,* 2026). Natural nutritional variation within germplasm is often substantial (Paras *et al.,* 2023; Indrabi *et al.,* 2024), the genetic architecture of major traits is increasingly well resolved (Jha et al., 2025), and gene editing can now modify multiple nutritional traits simultaneously in one background (Hong *et al.,* 2026). However, this literature is equally notable for its trade-offs: carotenoid dry matter pleiotropy in cassava (Villwock *et al.,* 2025), fruit-set penalties from multi-trait tomato editing (Choi *et al.,* 2025), and seasonal decline of transgenic provitamin A in ratoon banana crops (Tindamanyire et al., 2026) all caution against treating biofortification as simply additive. This review synthesizes the genetic basis of nutritional traits, compares conventional and biotechnological breeding strategies, examines regulatory mechanisms, evaluates GxE stability, and considers the biosafety/consumer landscape shaping deployment, prioritizing 2020 - 2026 literature weighted toward 2024 - 2026.

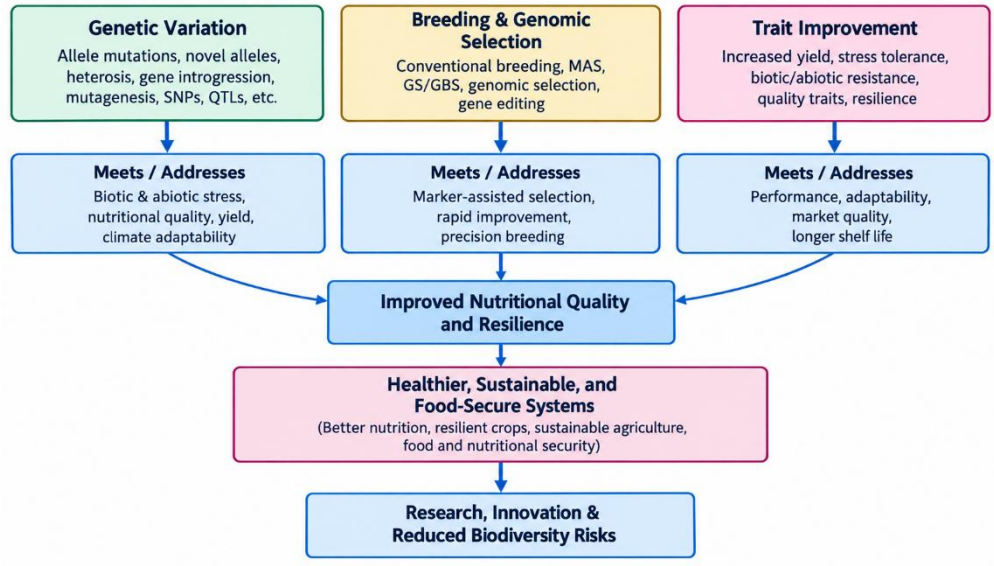


Figure 1. Conceptual framework linking genetic variation to improved nutritional quality in horticultural crops.

2. Nutritional Importance and Biofortification Potential

Fruits and vegetables supply the majority of dietary vitamin C, provitamin A, and folate in most diets. Biofortification, conceived initially for staple crops (Bouis & Welch, 2010; Nestel *et al.,* 2006), is now recognized as complementary in horticultural crops: reviews of fruit-crop strategies for iron, zinc, vitamin C, and beta-carotene enhancement across mango, banana, pomegranate, and citrus frame this as a sustainable, low-cost intervention (Ahmad *et al.,* 2026), while Bashir *et al.* (2026) argue fruit biofortification remains systematically under-studied relative to cereals despite naturally high bioactive content. This relevance extends beyond low-income settings: a scoping review found biofortification also holds promise as a food-based strategy in high-income countries, though evidence for real dietary impact there remains fragmented (Gulyas et al., 2025). Azeem *et al.* (2025) synthesize agronomic, breeding, transgenic, and editing strategies together, concluding no single approach is universally superior a conclusion reinforced experimentally where genetically biofortified potato receiving foliar zinc achieved far larger gains than either strategy alone (Zevallos *et al.,* 2024). *Tiozon et al.* (2026) propose AI-assisted genebank mining combined with marker-assisted selection and editing as the next frontier for repositioning biofortification as a food-systems-level strategy.

3. Genetic Basis of Nutritional Traits

Nutritional trait architecture spans single major-effect loci to highly polygenic traits. Carrot carotenoid accumulation is substantially controlled by the *Or* locus (*DcRPGE1*), which normally represses carotenoid biosynthesis via DcAPRR2; a natural promoter insertion truncates this repressor in domesticated carrots, and CRISPR knockout of the wild-type repressor boosts carotenoids further (Wang *et al.,* 2024). By contrast, strawberry ascorbic acid shows complex, environmentally variable QTL architecture despite a consistent candidate gene, *FaGGP* (Muñoz *et al.,* 2023). Heritability estimates guide tractability: ascorbic acid and phenolics show high heritability in guava (Paras *et al.,* 2023), and potassium, manganese, and zinc show heritabilities up to 74% in potato (Pandey *et al.,* 2023). Single-gene disruptions can exert outsized effects mutation in *BrFLS* redirects flavonoid flux to anthocyanins in Chinese cabbage (Zou *et al.,* 2024) while genomic selection captures polygenic variance even where causal architecture is unresolved, as in cassava provitamin A carotenoids (Esuma *et al.,* 2021). Wild germplasm remains an underexploited resource: watercress wild relatives harbour elevated glucosinolate/mineral variants (Qian et al., 2025), and pepper germplasm diversity aligns with cultivar type and geography (Indrabi *et al.,* 2024).

4. Conventional Breeding Strategies

Selection, hybridization, backcrossing, mutation breeding, and wide hybridization remain foundational. Tomato's domestication history illustrates both the power and the cost of intensive selection fruit size and shelf life improved at a documented expense to flavour and nutrient concentration that biofortification breeding must now reverse (Bai & Lindhout, 2007). Hybridization continues to generate transgressive nutritional gains: interspecific citrus hybrids exceed parental vitamin C, sugar, and acid profiles (Chavda *et al.,* 2026), and guava hybrids show useful nutraceutical segregation (Kashyap *et al.,* 2026). Mutation breeding, formalized as a mainstream methodology with over 2,250 released varieties

worldwide (Ahloowalia *et al.,* 2004), continues to generate nutritional diversity, as in an EMS eggplant mutant mapping anthocyanin-control genes (Luo *et al.,* 2023) and a large EMS pepper population with altered pigment profiles (Siddique *et al.,* 2020). Wide hybridization introgresses wild-relative alleles otherwise unavailable in cultivated germplasm, as demonstrated in okra (Suma *et al.,* 2023), and crop wild relatives more broadly are seen as an underused resource for iron/zinc biofortification under climate stress (Xu *et al.,* 2024). Genomic selection is increasingly integrated with, rather than replacing, these conventional structures, though concentrated in a few well-resourced crops (Lee *et al.,* 2024).

5. Marker-Assisted Breeding and Genomic Selection

Marker-assisted selection has reached practical maturity for some traits: *Or*-gene co-dominant markers in cauliflower enabled delivery of sixteen homozygous beta-carotene-enriched lines across maturity groups (Singh *et al.,* 2025b). Genomic selection adds value where traits are highly polygenic cassava pro vitamin A prediction reached r = 0.79–0.81 by combining multi-locus GWAS with ensemble models (Abincha *et al.,* 2026) while GBS-based GWAS in potato identified sixteen marker-trait associations for iron, zinc, copper, and manganese, including a chromosome-12 manganese locus explaining ~20% of variance (Singh *et al.,* 2026). Marker transferability across populations remains a practical constraint: validated cassava SNPs near *PSY2* remained robust for carotenoid content across populations, while dry-matter and cyanogenic-glucoside markers showed weaker, population-specific transferability (Anokye *et al.,* 2026). Genomic selection research overall remains concentrated in apple, strawberry, and tomato, leaving most vegetable crops underexplored (Lee *et al.,* 2024).

6. QTL Mapping and GWAS for Nutritional Traits

QTL mapping and GWAS, building on foundational interval-mapping methodology (Lander & Botstein, 1989), have resolved much of the genetic architecture underlying carotenoid, mineral, and amino-acid traits. In carrot, major QTL map to chromosomes 1, 3 (co-located with *Or*), and 6 (near *CYC-B*), with a KASP marker developed for practical selection (Shibaya *et al.,* 2022); combined GWAS and genomic prediction further dissect this polygenic architecture (Rolling *et al.,* 2025). In squash, GWAS identified three QTL and seven candidate genes for carotenoid content (López *et al.,* 2025). Amino-acid and protein GWAS in potato identified 78 loci with cysteine as the limiting amino acid (Rasheed *et al.,* 2025), while integrated GWAS, TWAS, and spatial transcriptomics in pepper identified AP2/PPR transcription factors as master regulators of carotenoid and flavour traits, subsequently validated by CRISPR knockout (Reddy *et al.,* 2025). Meta-QTL analysis across cranberry populations identified 22 stable cross-study loci (Maule *et al.,* 2024), underscoring that cross-population validation, not single-study QTL detection, gives the most breeding-relevant confidence.

7. Genomics, Transcriptomics, Proteomics, and Metabolomics

Pan-genome resources have expanded rapidly: a watermelon super-pangenome (138 genomes) identified a dosage-dependent copy-number variant controlling flesh-colour intensity via *ClFCI1* (Sun *et al.,* 2026), and a telomere-to-telomere carrot genome revealed 65 carotenoid-pathway genes, nine previously unidentified (Wang *et al.,* 2023). Multi-omics integration increasingly resolves tissue-specific regulation that sequence alone cannot: combined transcriptome-metabolome analysis clarified anthocyanin variation in strawberry flesh colour (Ren *et al.,* 2024), and integrated genomics in Chachiensis mandarin identified the enzyme CcOMT1 and an AP2/ERF regulatory network for polymethoxylated flavonoids while defining the optimal harvest window for bioactive content (Wen *et al.,* 2024). Proteomic evidence remains comparatively sparse but corroborative, as in a red- versus white-fleshed apple comparison identifying anthocyanin-regulatory proteins (Lautenbach *et al.,* 2025).

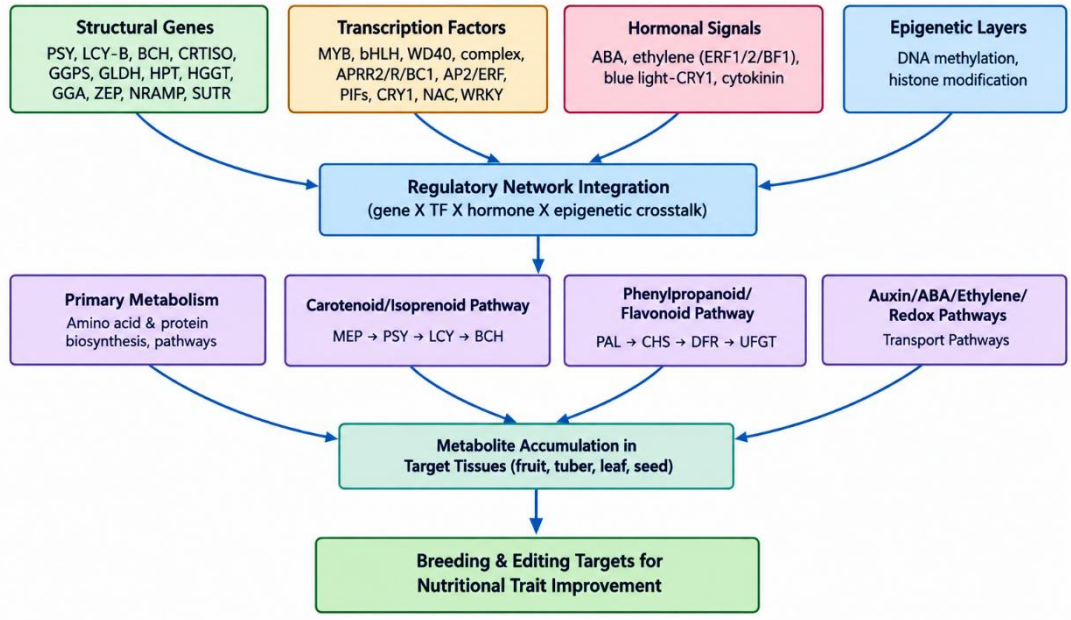


Figure 2. Integrated genetic and molecular regulatory framework governing nutritional trait accumulation in horticultural crops.

Table 3. Selected genes, transcription factors, and metabolic pathways governing nutritional traits in horticultural crops

Gene/TF/pathway component	Crop(s)	Trait/pathway	Functional role	Source
PSY (phytoene synthase)	Tomato, carrot, watermelon	Carotenoid biosynthesis	Rate-limiting step of carotenoid pathway flux	Duduit et al. (2022); Shao et al. (2026)
Or/DcRPGE1-APRR2	Carrot, cauliflower	Carotenoid accumulation	Represses/de-represses carotenoid biosynthesis and chromoplast development	Wang et al. (2024); Singh et al. (2025); Wrightstone et al. (2025)
IbbHLH25 / IbbHLH66	Sweet potato	Carotenoid biosynthesis	Promoter-variant-dependent activation of carotenoid genes	Wei et al. (2025)
MYB-bHLH-WD40 (MBW) complex	Tomato, strawberry, grape, potato, pear	Anthocyanin biosynthesis	Transcriptional activation of structural anthocyanin genes	Kong et al. (2026); Duan et al. (2025); Du et al. (2025)
VvMYB44-1	Grape	Anthocyanin repression	Suppresses MBW-driven anthocyanin synthesis under heat stress	Leng et al. (2025)
ERF.B2 / ERF.B5	Tomato	Ascorbate biosynthesis	Synergistic transcriptional activation of multiple ascorbate pathway nodes	Chen et al. (2025)
GGP1 / GPP	Tomato	Ascorbate biosynthesis	Catalyze D-mannose/L-galactose pathway flux toward ascorbate	Koukounaras et al. (2022)
GGH (gamma-glutamyl hydrolase)	Tomato	Folate retention	Reduced activity increases folate polyglutamylation/retention	Tyagi et al. (2023)
HPT / HGGT / gamma-TMT	Multiple crops	Tocopherol biosynthesis	Control homogentisate prenylation and tocopherol form conversion	Li et al. (2025c)
NAS (nicotianamine synthase) / Ferritin	Potato	Fe/Zn chelation and storage	Chelates and sequesters iron and zinc in tuber tissue	Cortelezzi et al. (2025)
StZIP2	Potato	Zinc transport	Enhances root growth and zinc transport efficiency	Fan et al. (2025)
SULTR gene family	Tomato	Selenium/sulfate uptake	Mediates selenate/selenite transport for Se biofortification	Yi et al. (2026); Wang et al. (2025)
SlGAD2 / SlGAD3	Tomato	GABA accumulation	Calmodulin-domain truncation removes auto-inhibition, raising GABA	Kim et al. (2025); Zhu et al. (2025)
BrFLS (flavonol synthase)	Chinese cabbage	Anthocyanin accumulation	Mutation redirects flavonoid flux toward anthocyanin branch	Zou et al. (2024)
MYB28 / GSTF11 / FMOGS-OX5	Brassica (mustard)	Glucosinolate biosynthesis	Regulate glucosinolate accumulation in seed and leaf tissue	Tandayu et al. (2022); Tu et al. (2025)

8. Gene Editing and Advanced Biotechnology

CRISPR/Cas editing now permits simultaneous multi-trait modification: multiplexed editing achieved combined vitamin/phytonutrient enhancement in a single tomato background (Hong et al., 2026), and targeted *SlGAD3* mutagenesis raised GABA 3.2 - 4.4-fold in commercial cultivars without agronomic penalty (Zhu *et al.,* 2025). Trade-offs are not universal but are real: combined *SlESK1-3*/*SlGAD3* edits raised sugar, GABA, and vitamin C but reduced fruit set via impaired xylem development (Choi *et al.,* 2025), whereas *SlLCYe*/*SlBCH* knockout raised beta-carotene 1.7 - 2.5-fold with no cost to lycopene or shelf life (Liu *et al.,* 2025b). Expanding Cas12/Cas13 toolkits broaden targetable sequence space (Liu *et al.,* 2025a; Li *et al.,* 2023a) and viral/viroid resistance applications protect tuber and fruit quality indirectly (Khoo *et al.,* 2024). Base and prime editing remain constrained chiefly by efficiency and specificity (Li *et al.,* 2023b; Vats *et al.,* 2024), though optimized delivery systems have raised dicot prime-editing efficiency to 38.2% of transformants in tomato (Vu *et al.,* 2024), with systematic reviews tracing four converging optimization strategies (Tian *et al.,* 2025). Transgenic approaches, foundational since Golden Rice's reconstitution of the provitamin A pathway in rice endosperm (Ye *et al.,* 2000; Paine *et al.,* 2005), continue to demonstrate strong nutritional gains in horticultural crops but remain constrained by regulatory and cultural-acceptance barriers (Shohael *et al.,* 2025), a tension examined further by product- versus process-based regulatory reviews (Pal *et al.,* 2025; Venkataraman *et al.,* 2025).

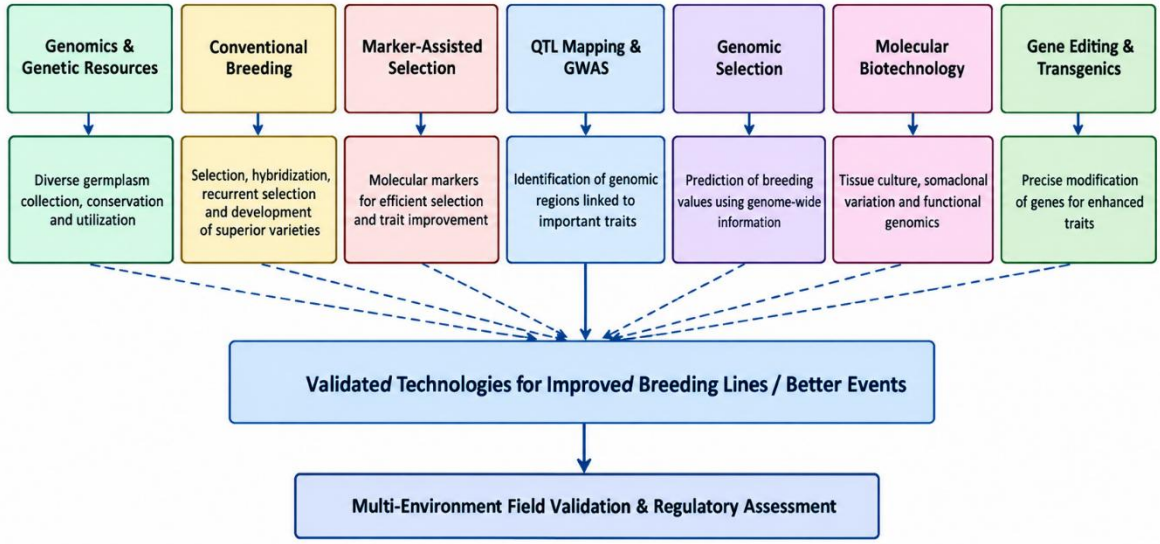


Figure 3. Integrated breeding-to-biotechnology pipeline for nutritional trait improvement in horticultural crops.

9. Vitamin and Provitamin Biofortification

Carotenoid biofortification builds on the pathway framework established by earlier biochemical work (Cunningham & Gantt, 1998), just as anthocyanin biofortification draws on classical flavonoid pathway genetics (Holton & Cornish, 1995); an early "CRISPR era" opinion piece correctly anticipated that editing pathway genes would outpace transgenics while flagging regulatory approval as the key bottleneck (Zheng *et al.,* 2021). The OR protein family acts as a DnaJ-like chaperone stabilizing phytoene synthase and is now a validated biofortification tool across tomato, potato, and rice (Wrightstone *et al.,* 2025). Multi-gene stacking in tomato shows *SlORHis* alone gives the strongest carotenoid boost, while *SlBHY* specifically enriches xanthophylls (Zhang *et al.,* 2024b), and hormonal/light signalling converges on carotenoid regulation, as in mango where blue-light-activated CRY1 blocks PIF5 repression of the transcription factor AGL5 (Zhang *et al.,* 2025b). The cassava carotenoid–dry matter trade-off arises from mediated pleiotropy rather than simple linkage, foreclosing simple recombination-based fixes (Villwock *et al.,* 2025), while transgenic provitamin A banana shows first-cycle gains that decline in later ratoons under seasonal stress (Tindamanyire *et al.,* 2026). Ascorbate, tocopherol, and folate biofortification rest on distinct entry points: ethylene response factors ERF.B2/B5 raise tomato ascorbate 140–149% (Chen *et al.,* 2025); *GGP1/GPP* overexpression achieved a threefold ascorbate increase without yield penalty (Koukounaras *et al.,* 2022); vitamin E gains follow overexpression of *HPT*/*HGGT*/gamma-*TMT* (Li *et al.,* 2025c); and the high-folate tomato landrace Periyakulam-1 achieves its phenotype through reduced GGH activity rather than enhanced biosynthesis (Tyagi *et al.,* 2023), while transgenic lettuce achieved a stable 3.4-fold folate increase across two field years (Queiroz *et al.,* 2025).

Table 1. Major nutritional traits in horticultural crops, representative crop systems, and their genetic basis

Nutritional trait	Representative crops	Genetic basis / key loci	Significance
Provitamin A carotenoids	Carrot, tomato, sweet potato, cassava, banana, mango, papaya, pepper	*Or*/*DcRPGE1-APRR2*, *PSY*, *LCYb/LCYe*, *BCH*, *IbbHLH25/66* (Wang et al., 2024; Wei *et al.,* 2025; Villwock *et al.,* 2025)	Reduces vitamin A deficiency; frequently trades off against dry matter/yield in root crops
Ascorbic acid (vitamin C)	Tomato, strawberry, pepper, citrus, guava	*GGP1/GPP*, *FaGGP*, *ERF.B2/B5* (Koukounaras *et al.,* 2022; Muñoz *et al.,* 2023; Chen *et al.,* 2025)	Antioxidant vitamin; QTL architecture is complex and environmentally sensitive
Tocopherols (vitamin E)	Tomato, pepper, leafy vegetables	*HPT*, *HGGT*, *gamma-TMT* (Li *et al.,* 2025c)	Lipid-soluble antioxidant; tissue-specific regulation still incompletely resolved
Folate	Tomato, lettuce	*GGH* (reduced activity raises retention); transgenic pathway stacking (Tyagi *et al.,* 2023; Queiroz *et al.,* 2025)	Field-stable transgenic gains demonstrated in lettuce
Iron and zinc	Potato, sweet potato, common bean, spinach	*NAS*, *FERRITIN*, *StZIP2*, GWAS loci on multiple chromosomes (Cortelezzi et al., 2025; Fan *et al.,* 2025; Mukamuhirwa *et al.,* 2025)	Bioavailability strongly modulated by anti-nutritional factors
Selenium	Solanum vegetables, general horticultural crops	Sulfate transporter (*SULTR*) family (Wang *et al.,* 2025; Yi *et al.,* 2026)	Agronomic and genetic strategies converge; largely a management-genetics interaction
Anthocyanins	Tomato, potato, grape, strawberry, pear, chilli, Chinese cabbage, yardlong bean	MYB-bHLH-WD40 complex, *ANT1*, *BrFLS*, repressor MYBs (Zou *et al.,* 2024; Zhang *et al.,* 2024a; Du *et al.,* 2025; Leng *et al.,* 2025)	Antioxidant pigments; heat stress can suppress accumulation via repressor TFs
Flavonoids and phenolics	Apple, citrus, mustard, general horticultural crops	Phenylpropanoid pathway genes, chromosome-16 bHLH locus in apple (Song *et al.,* 2025; Xu & Wang, 2025)	Broad health-relevant compound class with complex polygenic control
Glucosinolates	Brassica vegetables (cabbage, broccoli, mustard)	*MYB28*, *GSTF11*, *FMOGS-OX5*, *BnaC09.MYB28* (Tandayu *et al.,* 2022; Cai *et al.,* 2024; Tu *et al.,* 2025)	Tissue-specific regulation allows decoupling of desirable/undesirable accumulation
Protein and amino acids	Soybean, pea, potato, other legume vegetables	Seed-protein stability QTLs on chromosomes 10/18 (soybean); pleiotropic potato loci (Mitchell *et al.,* 2025; Rasheed *et al.,* 2025)	Cysteine often the limiting amino acid in tuber crops
Dietary fiber	Andean blueberry, mustard greens	Genetic mapping of cell-wall polysaccharide loci (Velasco Anacona *et al.,* 2026; Long *et al.,* 2026)	An underexplored nutritional trait relative to vitamins/minerals

10. Mineral Biofortification and Bioavailability

Iron and zinc strategies converge on shared transporter/chelator genes: NAS-plus-ferritin stacking raised potato tuber iron 2.1-fold and zinc 1.8-fold without yield penalty (Cortelezzi *et al.,* 2025), and *StZIP2* characterization offers a non-transgenic zinc-transport target (Fan *et al.,* 2025), while GWAS in Rwandan common bean identified loci for seed iron/zinc (Mukamuhirwa *et al.,* 2025). Selenium biofortification exploits overlap with sulfate-transport machinery (Wang *et al.,* 2025a), with SULTR gene family characterization in tomato offering direct breeding targets (Yi *et al.,* 2026). Genetic and agronomic biofortification act synergistically rather than merely additively: biofortified potato receiving foliar zinc achieved a 43% zinc increase versus 6% in a non-biofortified variety under the same treatment (Zevallos *et al.,* 2024). Bioavailability, not raw concentration, ultimately determines nutritional value: phytic acid, tannins, and other anti-

nutritional factors persist as key constraints (Samtiya *et al.,* 2020), and GWAS in spinach identifying oxalate-controlling loci represents a rare example of breeding for bioavailability rather than concentration alone (Xiong *et al.,* 2025).

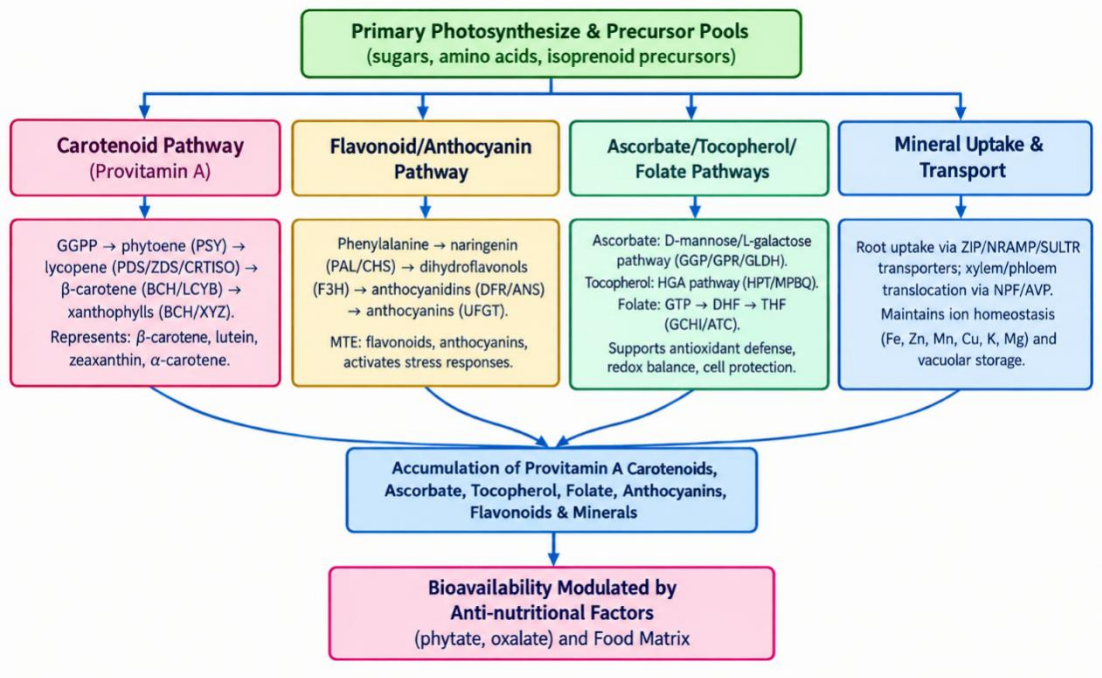


Figure 4. Major biosynthetic pathways underlying vitamin, mineral, and phytochemical accumulation in horticultural crops.

11. Phytochemical and Functional Nutrient Enhancement

Anthocyanin biosynthesis is governed by the conserved MYB-bHLH-WD40 (MBW) complex across tomato, strawberry, grape, and potato (Kong *et al.,* 2026; Duan *et al.,* 2025), while repressor transcription factors removable or silenceable as a breeding strategy include VvMYB44-1, which suppresses grape anthocyanins specifically under heat stress (Leng *et al.,* 2025). Applied markers now exist for tandem R2R3-MYB genes controlling potato tuber-flesh anthocyanin (Du *et al.,* 2025) and for *qANT5*/*VuANT1* controlling 56% of pod anthocyanin variance in yardlong bean (Zhang *et al.,* 2024a). Flavonoid and phenolic traits are similarly polygenic but occasionally tractable: an apple metabolomic GWAS found a single chromosome-16 bHLH locus explaining roughly one-third of phenolic variance (Song *et al.,* 2025). Protein and fibre traits remain comparatively nascent targets: soybean seed-protein-stability QTL on chromosomes 10 and 18 improve stability without yield penalty (Mitchell *et al.,* 2025), and genetic mapping in wild Andean blueberry and mustard greens provides early dietary-fibre breeding foundations (Velasco Anacona *et al.,* 2026; Long *et al.,* 2026). Tissue-selective glucosinolate regulators in Brassica allow decoupling of desirable leaf accumulation from undesirable seed accumulation (Tu *et al.,* 2025).

12. Improving Bioavailability and Reducing Anti-Nutritional Factors

Anti-nutritional factors phytic acid, tannins, saponins, protease inhibitors remain widespread constraints on mineral bioavailability, with fermentation, germination, and soaking the primary post-harvest reduction strategies (Samtiya *et al.,* 2020). Genetic approaches addressing bioavailability at the source remain rare but instructive: spinach GWAS for oxalate accumulation, which reduces calcium and iron bioavailability, offers markers for low-oxalate breeding (Xiong *et al.,* 2025). Agronomic and genetic biofortification interact directly with bioavailability outcomes foliar iodine/iron biofortification in tomato and cultivar-dependent uptake efficiency in vegetables both depend on genetically determined uptake traits that breeding could target more explicitly (Ikram *et al.,* 2024; Bandara & Dissanayaka, 2025). Because concentration-focused selection does not automatically improve and could plausibly worsen bioavailability where uptake and chelation pathways are linked, this remains an underexplored but consequential research gap.

13. Crop-Specific Advances

Tomato remains the most extensively engineered horticultural crop, with cultivar-dependent carotenoid profiles (lycopene- versus beta-carotene-dominant) increasingly subject to targeted CRISPR modification (Yoo *et al.,* 2026). Potato biofortification spans transgenic, marker-assisted, and editing strategies simultaneously, with diploid breeding proposed as a route around potato's challenging tetraploid genetics (Agrawal *et al.,* 2024; Li *et al.,* 2025b). Sweet potato shows high heritability for yield and quality traits across biofortified genotypes (Modak *et al.,* 2025). Brassica vegetables have been characterized as an "undervalued nutritional goldmine" for glucosinolates and carotenoids (Zhang *et al.,* 2024c), and large-scale spinach GWAS (3.4 million SNPs) identified over 2,000 loci for chlorophyll, oxalate, and iron-bioavailability traits (Ji *et al.,* 2024). Among fruit crops, interspecific citrus hybrids show transgressive nutritional gains (Chavda *et al.,* 2026), transgenic East African highland banana events combine elevated pro-vitamin A with acceptable agronomic performance (Buah *et al.,* 2025), and apple GWAS identified the MdDof2.4-MdPAT10 module regulating procyanidin accumulation (Li *et al.,* 2025d). Legume vegetables and spices remain comparatively underrepresented but

show clear potential, as in dry pea nutritional-trait characterization (Windsor *et al.,* 2024) and turmeric genotype evaluation for curcumin content (Das *et al.,* 2026).

Table 4. Selected 2020-2026 advances in biofortification of horticultural crops: crop, trait, methodology, and key findings

Crop	Trait targeted	Methodology	Key finding	Source
Tomato	Beta-carotene	CRISPR/Cas9 knockout of *SlLCYe*/*SlBCH*	1.7-2.5-fold higher fruit beta-carotene without reducing lycopene or shelf life	Liu *et al.* (2025)
Tomato	Multiple vitamins/phytonutrients	Multiplexed CRISPR/Cas9 editing	Simultaneous "stacked" enhancement of several nutrients in one genetic background	Hong *et al.* (2026)
Potato	Iron and zinc	Transgenic *NAS* + ferritin stacking	2.1-fold Fe and 1.8-fold Zn increase without yield penalty	Cortelezzi *et al.* (2025)
Cavendish banana	Provitamin A	Transgenic *ZmPsy1*/*MtPsy2a*/*PaCrtI*	Elevated carotenoids in initial crop cycle but declined in later ratoons under seasonal stress	Tindamanyire *et al.* (2026)
Cassava	Provitamin A carotenoids	Multi-locus GWAS + ensemble genomic prediction	Prediction accuracy r = 0.79-0.81 for root beta-carotene	Abincha *et al.* (2026)
Sweet potato	Iron and zinc	Organic amendments + microbial inoculants	~1.7-fold Fe and 2-fold Zn increase via genotype x management synergy	Noumsi-Foamouhoue *et al.* (2026)
Strawberry	Ascorbic acid	Multi-country QTL mapping	Favorable-allele stacking raised ascorbic acid by ~31%	Muñoz *et al.* (2023)
Lettuce	Folate	Transgenic pathway-gene expression	Up to 3.4-fold folate increase, stable across two field seasons	Queiroz *et al.* (2025)
Cauliflower	Beta-carotene	*Or*-gene co-dominant marker-assisted breeding	16 homozygous beta-carotene-enriched breeding lines across maturity groups	Singh *et al.* (2025)
Chilli/pepper	Carotenoids and capsaicinoids	GWAS (193 SNPs)	Candidate markers for pungency and carotenoid biofortification	Haile *et al.* (2023)
Watermelon	Flesh-color intensity (lycopene)	Super-pangenome (138 genomes)	Dosage-dependent CNV upstream of *ClFCI1* controls flesh-color intensity	Sun *et al.* (2026)
Yardlong bean	Pod anthocyanin	High-density genetic mapping	QTL *qANT5* explains 56% of variance; *VuANT1* functionally validated	Zhang *et al.* (2024a)

14. Genotype-by-Environment Interactions and Trait Stability

GxE interaction is among the most under-addressed dimensions of this literature. Onion nutritional composition varies significantly with site-specific soil chemistry and temperature even within one country (Imran *et al.,* 2025), and bitter gourd trials found environment responsible for over 70% of yield variation (Moharana *et al.,* 2025). The transgenic pro-vitamin A Cavendish banana case is the clearest example of instability in a genetically improved line itself: carotenoid accumulation was highest in the first crop cycle and declined in later ratoons, with promoter choice affecting environmental sensitivity (Tindamanyire *et al.,* 2026). AMMI and GGE biplot models are increasingly applied to identify genotypes that are both high-performing and stable, as in tomato (Tiwari *et al.,* 2025) and brinjal (Bhan *et al.,* 2026). Because most reported nutritional values derive from single-environment, single-season trials, they should be read as environment-specific data points rather than stable genotypic properties.

15. Challenges, Biosafety, Regulatory, and Consumer Considerations

Regulatory frameworks for genome-edited crops diverge sharply between process-based (EU) and product-based (Canada, Latin America) systems, creating trade barriers and discouraging R&D investment (Fernández Ríos *et al.,* 2025; Vengadesen *et al.,* 2025). Consumer awareness of gene editing lags behind awareness of conventional GM, and benefit information alone does not shift acceptance (Paudel *et al.,* 2023); Japan's early deregulation illustrates that regulatory permissiveness alone does not guarantee market uptake, since only a fraction of approved products have reached consumers (Ishii, 2025), while African consumer-perception research documents persistent skepticism and regulatory gaps even where nutritional need is greatest (Dolapo *et al.,* 2025). Farmer-level adoption is shaped by socioeconomic and institutional factors more than by variety performance alone (Samuel *et al.,* 2024), and governance failures not farmer knowledge deficits—were identified as the binding constraint on Uganda's biofortification scale-up (Alioma *et al.,* 2025); gender dynamics further shape adoption through women's control of household assets and seed access (Spain *et al.,* 2026). Intellectual property tensions between innovation incentives and breeder/farmer access remain unresolved (Amentae *et al.,* 2024), even as biofortification investment continues to show strong documented returns, up to seventeen to one in some transgenic case studies (Shohael *et al.,* 2025).

Table 5. Emerging technologies and future opportunities for nutritional improvement of horticultural crops

Emerging technology	Current stage	Opportunity	Key constraint
Graph pan-genomes and super-pangenomes	Demonstrated in eggplant, watermelon	Capture structural variation missed by single reference genomes	Computational/analytical complexity; germplasm coverage still incomplete
Multiplexed/base/prime gene editing	Rapidly advancing in tomato, potato	Stack multiple nutritional traits in a single event; scarless edits	Efficiency and delivery still limiting in many dicot species
AI-driven genebank mining	Emerging (proposed frameworks)	Accelerate identification of nutritionally valuable, underused germplasm	Requires standardized, digitized phenotypic/genomic genebank data
Spatial transcriptomics and multi-omics integration	Demonstrated in pepper, citrus	Resolve tissue-specific regulatory networks underlying nutrient accumulation	High cost; limited to well-resourced research programs currently
Synthetic biology-based pathway engineering	Early stage	Enable multi-trait, pathway-level nutrient enhancement beyond native pathway limits	Regulatory uncertainty; long path to field deployment
Genomic selection with ensemble/AI models	Increasingly applied (cassava, fruit/vegetable crops)	Improve prediction accuracy for complex polygenic nutritional traits	Requires large, well-phenotyped training populations
Principle-based/harmonized regulatory frameworks	Under active policy discussion	Reduce trade barriers and R&D disincentives for gene-edited biofortified crops	Political and international-harmonization challenges

16. Future Perspectives

Future priority should shift from single-gene discovery toward multi-environment, multi-cycle, and bioavailability-integrated breeding pipelines, given how often first-cycle or single-environment gains have proven unstable (Tindamanyire *et al.,* 2026; Villwock *et al.,* 2025). Genomic and multi-omics infrastructure remains concentrated in a handful of well-resourced crops (Sun *et al.,* 2026; Yu *et al.,* 2026) and should be extended to underrepresented legume, leafy, and spice crops. AI-assisted genebank mining and ensemble genomic prediction (Abincha *et al.,* 2026; Tiozon *et al.,* 2026) signal that data integration, not further gene discovery, is increasingly the binding constraint on genetic gain for polygenic traits. Regulatory harmonization and risk communication not further editing-precision improvements are likely the binding constraint on deployment (Vengadesen *et al.,* 2025), and bioavailability-focused breeding, exemplified by low-oxalate spinach work (Xiong *et al.,* 2025), deserves substantially more attention relative to concentration-focused breeding.

17. CONCLUSIONS

Genetic variation for nutritional traits in horticultural crops is substantial and only partially exploited, and the molecular basis of major traits particularly carotenoid and anthocyanin biosynthesis is now understood with sufficient precision to support targeted breeding and editing. Marker-assisted selection, genomic selection, and multi-omics integration have matured into practically deployed tools for at least a subset of crops, and gene editing now permits multi-trait nutritional stacking within single backgrounds. Yet trade-offs between nutrient concentration and yield or biomass recur across crop-trait combinations rather than representing isolated exceptions, genotype-by-environment instability is documented specifically in biofortified lines, and anti-nutritional factors continue to limit realized nutritional benefit. Regulatory and consumer-acceptance barriers increasingly represent the binding constraint on deployment. Closing this translation gap

requires breeding pipelines that treat multi-environment stability, bioavailability, and regulatory pathways as integral design criteria from the outset, rather than as downstream afterthoughts.

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