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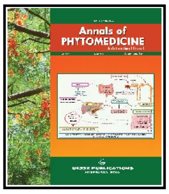

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Enhancing nutraceutical and pharmacological properties in vegetables: A genetic approach

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Abstract

Vegetables contain a diverse array of bioactive compounds, including phytochemicals like flavonoids, carotenoids, glucosinolates, and saponins. These compounds have been linked to reduction in inflammation, protection against chronic diseases, and the neutralization of harmful free radicals in the body, thereby supporting the body's defence mechanisms. However, the escalating global population presents a pressing challenge as malnutrition rates persist. In response, there is a critical need to address nutritional deficiencies through the enrichment of vegetables. To meet the demands of a growing populace and counter malnutrition effectively, there arises a necessity for the increased production of nutrient-rich vegetables. This involves implementing advanced techniques in crop improvement such as genetic engineering, marker-assisted selection (MAS), transcriptomics, proteomics, metabolic engineering and genome editing. With more precision, speed, multiplexing and versatility, CRISPR/Cas9 genome editing technology has emerged as an important tool to enhance the nutritional status of a crop comparing other techniques. Through this approach, broccoli rich in glucoraphanin content is developed by editing the MYB28 gene. So, by focusing on the production of nutrient-dense vegetables, we can strive to alleviate malnutrition and ensure a healthier, more nourished future for the expanding global population.

1. Introduction

Recent advances in medical and nutrition sciences have revolutionized the understanding of plants, transforming health, agriculture, and food concepts, attracting attention from both the public and health professionals (Rajat *et al.,* 2012). Phytonutraceuticals are plant-derived chemical compounds that promote health, providing antioxidant activity to protect cells from oxidative damage. Vegetables, including broccoli, spinach, tomatoes, and garlic, are essential for a healthy diet, providing essential nutrients like potassium, fiber, and vitamins A, E, and C. Folate is crucial for healthy red blood cell formation, especially for pregnant women and those with neural tube defects (Singh *et al.,* 2019a).

Traditional breeding methods are insufficient for addressing nutritional security issues, while molecular biology advancements like CRISPR/Cas offer an efficient approach to enhancing vegetable nutrition. RNAi technologies improve precision in enhancing resistance against pests, quality, and plant architecture. This article explores global genome engineering research utilizing CRISPR/Cas9 systems to create bioactive compound-rich vegetables, revolutionizing agriculture through expanded genome editing capabilities.

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2. Nutraceuticals from vegetable crops

Genetic modification techniques enhance vegetable nutritional content, address micronutrient deficiencies, and prevent diseases. Success depends on clear advantages and safety for growers and consumers. To mitigate bitterness in lettuce, scientists cloned the gene associated with sweetness and a taste-modifying protein known as miraculin from the berries' pulp in *Richadella dulcifica* (Sun *et al.,* 2006). When this gene was expressed in transgenic lettuce plants, it resulted in the production of a sweet-enhancing protein and a decrease in bitterness.

Most of the commonly available bioactive compounds like beta carotene, anthocyanin, tocopherol, folate and lycopene have been discussed mostly. The function of the neoxanthin synthase gene (BoaNXS) in carotenoid accumulation in Chinese kale (*Brassica oleracea*var *alboglabra*) was investigated. In three transgenic lines, the average carotenoid content was measured at 4.99 mg/g dry weight. Notably, neoxanthin and lutein exhibited significantly elevated levels in all three overexpressing plants (Jian*et al*., 2021). Also, among various transgenic eggplant lines generated by editing the phytoene synthase (crtB) gene, one line exhibited a β-carotene content of 1.50 μg/g fresh weight (FW), which is 30 times greater than the β-carotene level found in unmodified fruits (0.05 μg/g FW) (Mishiba *et al.,* 2020). Gaining information on some of the minor compounds that have the potential to overcome nutritional requirements might be an eye-opening for a healthy lifestyle. The bioavailability and biosynthesis of different bioactive compounds in vegetables are given in Table1 and Figure 1, respectively.

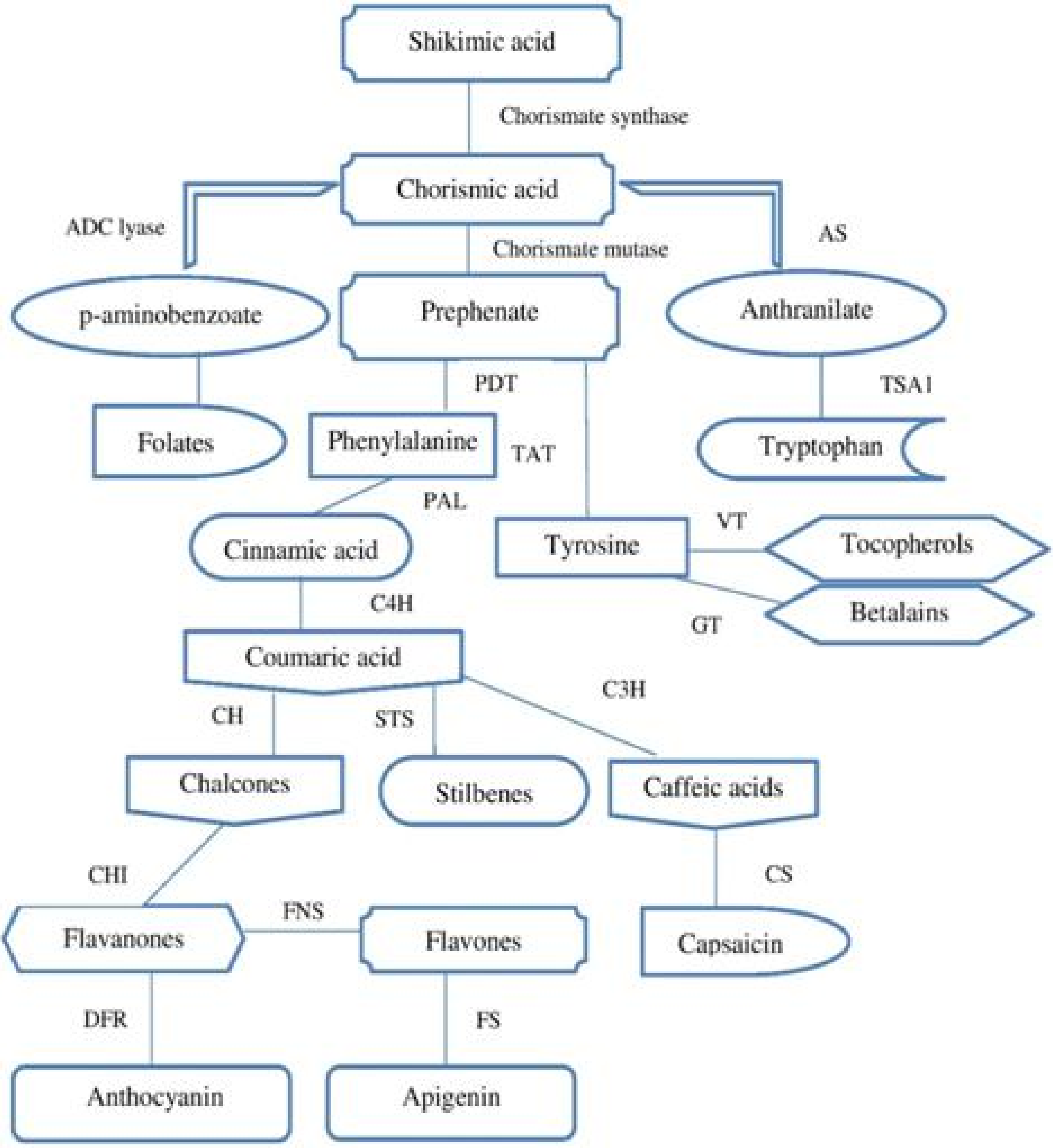

Figure 1: Biosynthesis of bioactive compounds present in vegetables.

AS-Anthranilate synthase; PDT-prephenatedehydratase; CHS-Chalcone Synthase; FS-Flavone synthase; PAL-Phenylalanine ammonia lyase; VTE4-d-tocopherolmethyltransferase; FNS-Flavone Synthase; C4H-Cinnamate-4-hydroxylase; TSA-tryptophan synthase; TAT-Tyrisine aminotransferase; C3H-Coumaric acid-3-hydroxylase; GT-Glucosyltransferase; DFR-DihydroFlavonolReductase; CS-Capsaicin Synthase; CHI-ChalconeIsomerase; ADC lyase -4-amino-4-deoxychorismic acid lyase; STS-Stillbene Synthase.

Table 1: Bioavailability of nutraceuticals in various vegetable crops

Vegetable	Compound	Bioavailability	Reference
Chinese cabbage	Apigenin	187.0 mg/kg	Miean *et al.,* 2001
Bell pepper	Apigenin	272.0 mg/kg	
Garlic	Apigenin	217.0 mg/kg	
Snake gourd	Apigenin	42.4 mg/kg	
Celery	Apigenin	338.5 mg/kg	
Broccoli	Sulforaphane	214 µg/g DW (stems) to 499 µg/g DW (inflorescences)	Campas-Baypoli *et al.,* 2009
Purple cabbage	Sulforaphane	101.99 µg/g DW	
Green cabbage	Sulforaphane	7.58 µg/g DW	
Cauliflower	Caffeic acid	1.00 mg/100 g FW	Birkova *et al.,*2020
Eggplant (Purple)	Caffeic acid	0.38 mg/100 g FW	
Olive (Black)	Caffeic acid	2.10 mg/100 g FW	
Olive (Green)	Caffeic acid	1.33 mg/100 g FW	
Tomato, whole	Caffeic acid	0.45 mg/100 g FW	
Carrot	Caffeic acid	0.02 mg/100 g FW	
Potato	Caffeic acid	1.62 mg/100 g FW	

Table 2: Genes identified in vegetable crops for nutraceutical development

Vegetable	Nutrient/Nutraceutical compound	Gene/Tanscription factors	Tools	References
Celery	Apigenin	AgFNS	-	Tan *et al.*, 2017
	Apiin	UGT94AX1	Phylogenetic analysis	Yamashita *et al.*, 2023
Garlic	Allicin	*ISA1*, *ISA2*	Phylogenetic analysis	Sayadi *et al.*, 2020
Chilli	Capsaicin	CcMYB24 (*C. chinense*), CcPun1	*Agrobacterium*-mediated transformation	Zhang *et al.*, 2022
		AT3	*Agrobacterium*-mediated transformation	Arce-Rodriguez and Ochoa-Alejo,2015
Broccoli	Sulforaphane	BoMY, BoHMT	*Agrobacterium*-mediated transformation	Wu *et al.*, 2023a
Cabbage	Glucosinolate	CYP83 family and CYP79B and CYP79F subfamily	Sequencing analysis	Wang *et al.*,2023a
Tomato	High flavonoids	Hqt	CRISPR/Cas	D'Orso *et al.*, 2023
		SlDQD/SDH2	CRISPR/Cas9	Wang *et al.*, 2023b
	Caffeic acid	SlCOMT1	*Agrobacterium*-mediated transformation	Ge *et al.*, 2023
Chilli	Flavonoid	CaMYB12-like	*Agrobacterium*-mediated transformation	Wu *et al.*, 2023b
Allium fistulosum	Flavonoid	AfF3H	Genome wide characterization	Xu *et al.*, 2023

3. Biosynthesis and enhancement of nutraceuticals through genetic approach

3.1 Apigenin

Apigenin, a dietary flavonoid found in vegetables like Parsley, Chamomile, Celery, Vine spinach, Artichoke and Oregano is known for its anti-inflammatory, antidiabetic, anticancerous, chemoprevention, blood pressure reduction, and potential reduction in Alzheimer's disease, amnesia, and depression (Salehi *et al.,* 2019).

3.1.1 Biosynthesis of apigenin

The interaction of 4-coumaroyl-CoA with malonyl-CoA creates chalconaringenin (the backbone of flavonoids) with the presence of chalconesynthase, which is said to be a crucial enzyme for the biosynthesis of flavonoid (Wang *et al.,* 2022). Chalcone, an isomerase helps in the spontaneous cyclization of chalconaringenin (main intermediate chalconoid) into naringenin (Singh *et al.,* 2019b). Naringenin is then converted into apigenin with the help of the enzyme flavone synthase (Sharma *et al.,* 2019) (Figure 2a).

3.1.2 Genes responsible for apigenin synthesis

The study reveals that in AgFNS transgenic celery, anthocyanin content in petioles is lower but apigenin content is higher, with up-regulated genes and down-regulated genes, providing insight into the function of the AgFNS gene in celery biosynthesis (Yan *et al.,* 2020). Table 2 represents genes identified in vegetables for nutraceutical development.

3.2 Allicin

Allicin, an organosulfur compound found in garlic cloves, is a defensive compound with antibacterial, antifungal, and antioxidant properties. It is produced by the enzyme allinase when garlic is chopped or crushed.The chemical structure of the compound allicin is given in Figure 2 (b). Allicins are found predominantly in garlic (*Allium sativum* L.) and onion which has a unique flavourand medicinal effects that can be conferred by most Allium species having high concentrations of S-alk(en)yl- L-cysteine sulfoxides (ACSO) (Sheikh-Raisuddin *et al.,* 2018; Sun *et al.,* 2020). This allicin have several biological properties such as antibacterial, antifungal and antioxidant and it is also used to treat arteriosclerosis.

3.2.1 Biosynthesis of allicin

ACSO, a stable source of diallylthiosulphinate (allicin) in garlic tissue, aids in the biosynthesis of compounds responsible for allium flavour, with allinase enzyme playing a crucial role (Stoll and Seebeck, 1947).

3.2.2 Genes responsible for allicin synthesis

The presence of diallyl disulphide and diallyl trisulphide is consistent with the expression of AcALL gene in stems, roots and leaves of tillering onion which is responsible for allinase enzyme (Yang *et al.,* 2023). CDS-deletion and frame shift mutation in a distinct FMO1 gene can be a reason for the strong odour present in the wild species of chinese chives (Xia *et al.,* 2022). Chemical structure of betaine is given in Figure 2c.

3.3 Betaine (trimethyl glycine)

Betaine, a sweet alkaloid found in beets, spinach, and whole grains like quinoa, wheat, oat brans, brown rice, and barley, belongs to the alpha amino acid class and was first isolated from sugar beet sap. It comes in two types, *viz.,*betaine namely alkyl betaines and alkyl amido propyl betaines (Betaine Global Market Report, 2023).

3.3.1 Uses

Glycine betaine, extracted from sugar beet, is used in various industries including cosmetics, pharmaceuticals, healthcare, cleaning, agriculture, food, beverages and cattle feed (Bunkar *et al*., 2020). It also helps maintain osmotic equilibrium in mammals by acting as an osmolyte in the kidney's inner medulla. The global market value of Betaine was 3.3 billion dollars in 2018 and is expected to reach 4.84 billion by 2027 (Betaine Global Market Report, 2023).

3.3.2 Betaines in stress tolerance

Glycine betaine is required for the formation of *S*-adenosylmethionine (SAM) and methionine which is considered an important source of methyl groups (Barak *et al.,*1996). By protecting and enhancing the photosynthetic apparatus, Betaine aldehyde dehydrogenase (BADH) and flavodoxin (Fld), increase the stress tolerance of different plant species and maintain their production under stressful situations. Hence these are considered multifunctional transgenes (Niazian *et al.,* 2021).

3.3.3 Enhanced betaine production

The tomato plants derived from a construct incorporating BvADHα gene through *Agrobacterium*-mediated transformation exhibited elevated levels of betanin compared to those from a construct lacking this gene (Grutzner *et al*., 2021).

3.4 Capsaicin

Capsaicin, the major active ingredient of chilli pepper, may play a "dual role" in tumourigenesis, acting as a carcinogen or as a cancer preventive agent (Zhang *et al*., 2020). It is a hydrophobic volatile compound exhibiting antimicrobial activity against various microorganisms. Chilli pepper extract and its bioactive compounds are reported to have various pharmacological effects, such as antibacterial, antioxidant, pain-relieving, and anti-inflammatory effects. The capsaicin content in chilli peppers is variable and ranges from 0.1% to 1% of the fruit weight (Xiang *et al*., 2021). Arthritis reducing effect of capsaicin has been reported in animal studies (Rani *et al.,* 2023). However, the main ingredient of chilli peppers, capsaicin, remains controversial. Recent studies have shown that capsaicin is a double-edged sword. It has potential biological activities at low concentrations, but it tends to produce adverse effects at high concentrations (Xiang *et al*., 2021). Chemical structure of capsaicin is presented in Figure 2d.

3.4.1 Genes involved in capsaicin pathway

About 50 genes involved in capsaicin metabolism have been identified through sequencing, including GPMP, COMT, pAMT, AT, BCAT, Kas, FatA, ACS, LBP and other metabolic pathway genes. Silencing these genes is identified to decrease capsaicin content (Zhang *et al.* 2022).

3.5 Caffeic acid

Caffeic acid (3,4-dihydroxy-cinnamic acid) is an organic compound and a potent antioxidant. It is found in a wide range of plants (cauliflower, cabbage, tomato, carrot, potato, kale and radish) though it is present in higher concentrations in plantation crops like coffee. Caffeic acid is a type of polyphenol, a class of micronutrients known for their antioxidant properties. The chemical structure of caffeic acid is presented in Figure 2e.

Caffeic acid, with a recommended dose of cinnamates ranging from 0 to 1 g, is believed to improve skin elasticity, reduce wrinkles, and possess strong antioxidant activity. It also increases collagen production, prevents premature ageing, and has antimicrobial properties (Birkova *et al.,* 2020).

3.5.1 Biosynthesis of caffeic acids

In potato, by the phenylpropanoid pathway, two important phenolic acids, *viz*., chlorogenic acid (CGA) and caffeic acid (CA) are produced. CSE (caffeoylshikimate esterase) is necessary for CA production. For lignin synthesis, ferulic acid is the precursor for which CA serves as a substrate through the action of caffeic/5-hydroxyferulic acid O-methyltransferase (COMT I). From feruloyl-CoA (which is necessary for lignin and suberin biosynthesis) via caffeoyl-CoA O-methyltransferase (CCoAOMT), caffeoyl CoA is synthesized.

3.5.2 Vegetables improved with high caffeic acid content

Transgenic potato tubers show a fourfold increase in caffeoylquinates, flavonols, and anthocyanin pigments due to *Agrobacterium tumefaciens* mediated transformation (Rommens *et al.,* 2008). Transgenic tomato seeds also show increased Melatonin content and salt tolerance, compared to wild-type plants (Ge *et al.,* 2023).

3.6 Glutathione

Glutathione, produced in the liver, is essential for tissue building, repair, and protein synthesis. It is found in bulb crops like garlic, vegetables like watermelon, crucifers and green leafy vegetables (Abdussalam *et al.,* 2021**)**. The amino acids, *viz.,* glycine, cysteine and glutamic acid are the source for the synthesis of glutathione. In the human body, it is produced in the liver and itself involved in many metabolic processes, *viz.,* tissue building and repairing and synthesis of proteins necessary for body and immune system functions (Gould and Pazdro, 2019). Figure 2f shows the chemical structure of glutathione.

3.6.1 Genes involved in glutathione synthesis

Glutathione S-transferases (GSTs) are essential enzymes in metabolic processes and glucosinolate biosynthesis. They play a significant role in plants undergoing oxidative stress, drought, and salinity. In carmine radish, GST genes encode anthocyanin transporters and help defend against heavy metal stresses. Understanding GST family functions can improve radish breeding programs (Gao *et al.,* 2020).

3.7 Sulforaphane

Sulforaphane (SFN) is also known as 1-isothiocyanato-4-(methylsulfinyl) butane. It is an aliphatic isothiocyanate for which the precursor is glucoraphanin. Cruciferous vegetables that mainly contain glucoraphanin are broccoli, cauliflower, brussels sprouts and cabbage (Panjwani *et al.,*2018; Pidigam *et al*., 2022).

3.7.1 Biosynthesis of SFN

With the help of the myrosinase enzyme (present in plants), SFN biosynthesis occurs through a hydrolysis reaction, which together with the epithiospecifier (ESP) protein in an inactive form leads to the formation of SFN. Conversely, SFN nitrile is synthesized, when the ESP is in active form and combines with myrosinase enzyme. Sulforaphane is available in all cruciferous vegetables like kale, cauliflower, kohlrabi and broccoli. Broccoli is the best source known for sulforaphane and its sprouts may be 25 times more potent than raw broccoli. Heating broccoli will deactivate the enzyme that produces sulforaphane (Bowen-Forbes *et al*., 2023).

3.7.2 Vegetables improved with high sulforaphane content

The study introduced FMOGS-OX2, MAM1 and myrosinase genes to broccoli, enhancing SFN biosynthesis. Transgenic plants showed higher SF content compared to wild type, with results ranging from 1.7-3.4 to 3.7-fold.However, with all three genes, the SFN contents in transgenic plants improved by 1.86-5.5fold (Cao *et al.,* 2021).

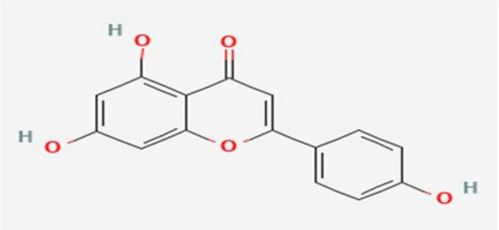

Figure 2a: Apigenin

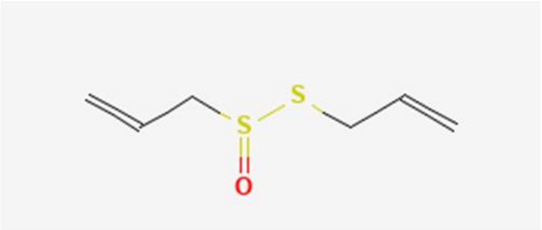

Figure 2b: Allicin

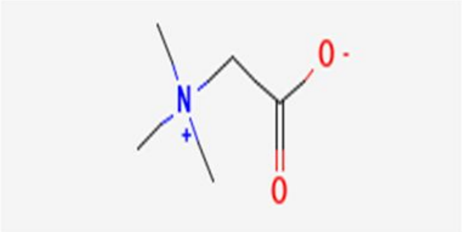

Figure 2c: Betaine

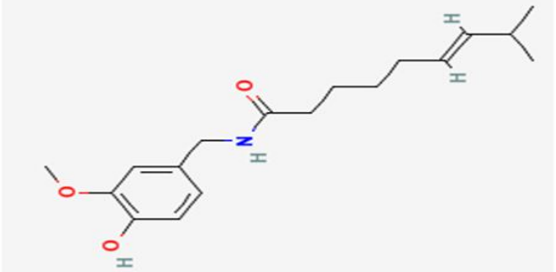

Figure 2d: Capsaicin

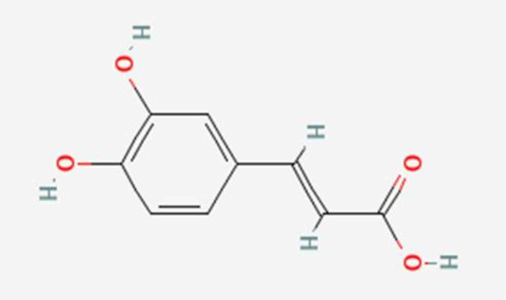

Figure 2e: Caffeic acid

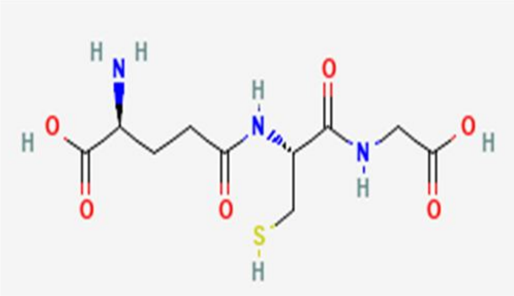

Figure 2f: Glutathione

4. Conclusion

Nutritional qualities and associated health benefits of vegetable crops becoming important criteria for their increase in consumer's diets. In this respect, breeding programmes for improving the content of nutrients are becoming more important for breeders. Recent approaches like molecular breeding and genetic manipulation emerge as efficient tools which can attain nutraceutical improvement in vegetables in the coming years. The key genes or genes regulating the molecular pathways are being genetically engineered or edited to develop phenotypically improved crop plants. Concentrating on the pathway of nutraceuticals can provide more information on the enzymes and genes involved in its biosynthesis. Genome sequencing plays a major role in identifying different genes engaged in the nutraceutical development pathway. One such example is through CRISPR/Cas9 editing of SlALMT9 (Al-activated malate transporter), researchers achieved increased malate levels in tomatoes Additionally, the levels of the nonproteinogenic amino acid GABA have been found to rise in tomato leaves and fruits. Understanding it deeply can provide more insights into its development. Combining more technologies like proteomics, metabolomics, GWAS (Genome-wide association studies) and CRISPR-Cas (Clustered regularly interspaced short palindromic repeats), faster development of nutraceutical rich vegetables can be developed that meets the global demand for nutrient deficiency.

Future prospects

Overall, genetic approaches hold significant promise for improving the nutritional quality, functional properties, and agronomic traits of vegetable crops, thereby contributing to global efforts to address malnutrition, improve public health, and promote sustainable food systems. However, continued research, stakeholder engagement, and ethical considerations are essential to harness the full potential of genetic approaches for nutraceutical development in vegetable crops in a responsible and sustainable manner.

Conflict of interest

The authors declare no conflicts of interest relevant to this article.

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