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GENE EDITING DRIVEN PRECISION BREEDING IN *FRAGARIA*: CURRENT PROGRESS AND FUTURE PROSPECTS

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ABSTRACT

Advancements in molecular genetics have identified important gene families like SWEET sugar transporters, LOX gene family, the transcription factor FvSTOP1, and FveIPT2 gene which are essential for sugar accumulation, anthocyanin production, handling plant resilience, and improving fruit quality respectively. In this review paper, we aimed to highlight the crucial role of strawberry biology and genetics, that lays the groundwork for future breeding and gene editing initiatives aimed at improving strawberry yield, fruit quality, and resilience to abiotic and biotic stress. Strawberries (*Fragaria spp*.), part of the Rosaceae family and known for their complex polyploidy, are appreciated worldwide for their bright color, unique aroma, and excellent nutritional value. Despite their widespread appeal and versatility in both fresh and processed options, strawberry farming encounters issues such as limited genetic diversity and vulnerability to various biotic threats including root pathogens (*Phytophthora*, *Verticillium*), leaf diseases, and anthracnose. The SWEET gene family manages two-way sugar transport, crucial for fruit development and flavor. FvSTOP1 controls anthocyanin production, linking fruit color to stress tolerance. FvLOX expression varies significantly with abiotic stresses like temperature, drought, and salinity, suggesting a role in plant resilience. FveIPT2 is a housekeeping gene that boosts metabolite levels and maintains growth. Manipulating these qualities presents an opportunity to enhance the nutritional and organoleptic characteristics of strawberries via genetic modification. Genome editing with CRISPR/Cas9 serves as a powerful method for enhancing the nutritional qualities of fruits and berries.

Keywords **:** CRISPR/CAS, Gene editing, Genetic regulation, Strawberry enhancement.

Introduction

Strawberries belong to the Rosaceae family, the Rosoideae subfamily, and the *Fragaria* genus. The *Fragaria* genus consists of nine diploid species, two tetraploid species, one hexaploid species, and four octoploid species. Each strawberry flower has multiple pistils, with each one featuring its own style and stigma connected to the receptacle (Palei *et al*., 2015) Comparative genetic mapping revealed significant macrosynteny and colinearity between the genomes of *F. ananassa* and *F. vesca*, implying that molecular studies performed in the diploid vesca are probably relevant to the octoploid *ananassa* (Shahan *et al*., 2019)

Strawberries are recognized for their bright red hue, distinctive aroma, and unique liquid texture. They are typically consumed fresh or incorporated into dishes like ice cream, milkshakes, and fruit preserves (Afrin *et al*., 2016). In many regions, strawberries are also enjoyed as dried fruit. These berries are rich in essential nutrients vital for human health, including protein, calcium, potassium, iron, copper, vitamin C, fiber, flavonoids, autocianidin, phytochemicals and antioxidants. Their incorporation in processed forms like cooked and sweetened conserves, jams, jellies, frozen whole berries, or sweetened juice extracts and flavorings, as well as their role in producing a diverse range of other processed goods, has established them

as one of the most favored berry crops, surpassing the distribution of any other fruit (Banerjee *et al*., 2023) At present, the strong emphasis on high standards means that both the flavor and aroma of fruit are critically evaluated, leading to increased focus on developing varieties with enhanced fruit aroma. The aromatic profile of strawberries is quite intricate, encompassing over 350 volatile compounds, including esters, furanones, terpenes, aldehydes, ketones, alcohols, and sulfur compounds. Furanones are the most significant contributors to the aroma of strawberry fruit, specifically furaneol (2,5-dimethyl-4-hydroxy-3(2H)-furanone) and its derivative mesifurane (2,5-dimethyl-4-methoxy-3(2H)-furanone) (Lyzhin *et al*., 2020) In vitro research suggests that phenolic compounds found in berries possess a variety of biological properties, including anti-cancer, antioxidant, anti-inflammatory, and regulatory effects on cells.(Mukherjee & Gantait, 2024) These anti-cancer properties arise through multiple mechanisms, such as the antioxidant effects of berry phenolics that protect DNA from harm, as well as other actions beyond just anti-oxidation. The biological functions of phytochemicals in strawberries involve the regulation of phase-II enzymes and the modulation of gene expression alongside subcellular signaling pathways related to cell growth, the formation of new blood vessels, and apoptosis (programmed cell death). Although numerous studies have reported on the anti-cancer effects of specific phenolics identified in strawberries.

In contrast to its relatives in the rosaceous family, the small herbaceous strawberry grows quickly and yields fruit in a short time. It can be readily propagated clonally through runners or by separating vegetative propagules known as branch crowns. These characteristics make strawberry a valuable model for research on genes derived from other crops that require extensive space and have long juvenile stages (Carvalho *et al*., 2016) Runners are frequently utilized in the vegetative propagation of strawberries to grow plants that are true to their type. A considerable number of runners and appropriate planting material are essential for successfully cultivating strawberries. (Anuradha *et al*., 2016) (Banerjee *et al*., 2023) Efforts have been made to enhance strawberry production in order to satisfy the need for better yields, larger fruit size, and superior quality characteristics. Nevertheless, the limited genetic diversity of cultivated strawberries, along with the polyploidy of the species, limits the effectiveness of conventional breeding techniques.

Strawberry plants rely on the length of daylight, with varieties classified as long day, short day, or day neutral. Many European nurseries cultivate several million plants annually using in vitro methods, which effectively address issues related to soil fungal flora that can significantly harm strawberry crops. Additionally, tissue-cultured plants appear to generate more runners from each mother plant within a shorter timeframe.

Biotic Stressors and Disorders in Strawberry Crops

Various soil pathogens can harm strawberry roots, leading to declines in vigor and, eventually, plant death. Two prevalent issues worldwide are red stele or red core, which is caused by *Phytophthora fragariae Hickman*, and *Verticillium* wilt, resulting from *Verticillium albo-atrum* and *V. dahliae*. Additionally, black root rot is common and arises from a combination of organisms, including *Pythium*, *Rhizoctonia*, and the root lesion nematode (*Pratylenchus penetrans*). Fumigation has been commonly used to manage soil pathogens; however, the upcoming prohibition of methyl bromide fumigation has triggered a greater interest in creating resistant cultivars. Among the foliar diseases, three are highly prevalent and can inflict significant harm: leaf blight [*Phomopsis obscurans*], Ramularia leaf spot [*Mycosphaerella fragariae*], and leaf scorch [*Diplocarpon earliana*]. Powdery mildew (*Sphaerotheca macularis*) is also present throughout most of the strawberry-growing regions, although it seldom results in economic loss. Angular leaf spot, caused by *Xanthomonas fragariae*, is an increasingly urgent issue for strawberries globally. Anthracnose is a widespread issue in strawberries, leading to various symptoms such as fruit rot, crown rot, and lesions on the stolons, petioles, and leaves. The anthracnose diseases affecting strawberries are attributed to *Colletotrichum fragariae* and *C. acutatum*. (Fig.1) Plants encounter various abiotic stresses during their growth cycle. Abiotic stress encompasses cold, heat, drought, salt stress, and other conditions. When subjected to abiotic stress, strawberry growth and nutrient uptake can be adversely affected, leading to reduced yield. Thus, enhancing strawberry's tolerance to these stresses to improve both yield and quality represents a significant challenge (Palei *et al*., 2015).

Materials and Methods

This work utilized secondary data obtained from articles, research papers, books, and reports that are accessible online. In addition, standard online databases like Google Scholar, PubMed, Research gate, Science Direct, were examined. The search items employed were CRISPR/CAS, Gene editing, Genetic regulation, Strawberry enhancement, etc.

Key Genes Driving Strawberry Enhancement

SWEET Gene Family

The SWEET gene family represents a newly identified set of sugar transporters essential for both plants and mammals (Lin *et al*., 2024). It refers to a class of bidirectional sugar transporters that play a vital role in essential physiological processes including plant growth, development, and the response to biotic and abiotic stresses (Du *et al*., 2024). SWEET proteins are structurally similar and function as energy-independent sugar transporters, characterized by two MtN3/saliva transmembrane domains. The first identified member of the SWEET family, MtN3, was found in the symbiotic relationship between the legume *Medicago truncatula* and *Rhizobium*. Further research revealed that SWEET proteins function as transporters for sucrose and fructose. During interactions with biological stress, plants typically adjust their sugar levels by upregulating or downregulating SWEET gene expression in response to various stresses. The involvement of SWEET genes in stress responses has been investigated in detail primarily in rice. The OsSWEET11 gene in rice has been shown to inhibit the growth of bacteria responsible for blight by regulating transcription. FvSWEET1, FvSWEET3, and FvSWEET4 have all demonstrated responses to various stress types, while FvSWEET10 only reacted to bacterial stress (*Phytophthora cactorum*) and fungal stress (*Botrytis cinerea*), but not to viral stress (SVBV). Notably, viral infection did not trigger expression of FvSWEET10, likely because the FvSWEET10 gene does not respond to viral stress. Research indicates that both bacterial and fungal symbionts, as well as pathogens, can stimulate the expression of various SWEET genes by releasing effector proteins that bind to and activate these genes (Lin *et al*., 2024). The SWEET protein is crucial for sugar transport, and understanding how sugar interacts with SWEET transport can enhance fruit quality. In a prior investigation, researchers identified members of the SWEET gene family in *Fragaria* × *ananassa* 'Camarosa' and thoroughly analyzed their molecular characteristics and expression patterns. Higher plants possess numerous SWEET gene family members, and various studies have documented the SWEET gene family such as in Arabidopsis thaliana, rice, maize, tomato, *Brassica rapa*, garlic, grapes, apples, litchi, watermelon, *longan*, jujube, *Bletilla striata*, *Dendrobium officinale*, and rose. The octoploid strawberry *(Fragaria* × *ananassa Duch*.) is currently the predominant cultivar, valued for its vibrant red color, delightful taste, and high nutritional content. The accumulation of sugars is crucial for fruit quality, yet some strawberry cultivars exhibit relatively low sugar content, which hinders the advancement of the strawberry industry to a degree. Currently, there has been limited research on the SWEET gene family in strawberries. The study conducted by Tian et.al predicts that FanSWEET genes are located in the plasma membrane, vacuole, chloroplast, endoplasmic reticulum, and Golgi apparatus, suggesting their involvement in various plant physiological processes. Their findings indicated that during the small green fruit stage, FanSWEET14 and FanSWEET15a were the most highly expressed genes. However, the expression levels of these genes gradually diminished as the fruits developed, exhibiting a negative correlation with sugar accumulation in the fruit. The expression of FanSW EET2a/3b/5a/17a remained consistently low throughout the fruit development of 'Yanli' strawberry, having minimal impact. Their study lays the groundwork for additional research on the FanSWEET gene family in strawberries and SWEET genes in other species (Du *et al*., 2024).

LOX Gene Family

Currently, the LOX gene family has been explored in numerous plant species, including Arabidopsis, rice, radish, and pear. However, there is currently no comprehensive information available regarding the genome-wide identification and characterization of strawberry LOX gene family members. In a prior investigation, they conducted a genome-wide analysis to identify LOXs in the diploid woodland strawberry (*Fragaria vesca*), resulting in the identification of 14 FvLOX members. They examined the expression levels of FvLOXs in response to various abiotic stresses (low temperature, high temperature, drought, salinity) and treatments with exogenous plant hormones (salicylic acid, methyl jasmonate, abscisic acid) (LI *et al*., 2022).

The FvLOX gene exhibited expression in different tissues and showed varying degrees of response to low temperature, high temperature, drought, salinity, and ABA, suggesting that the FvLOX gene potentially plays a regulatory role in coping with abiotic stress. Previous research indicated that FvLOX1 and FvLOX8 were prominently expressed in the roots, while FvLOX1, FvLOX8, AtLOX1, and AtLOX5 are categorized within the 9-LOX subfamily, implying they might share similar roles in the roots. It was also identified that FvLOX3 and FvLOX10 are highly expressed in leaves and flowers, where FvLOX3, FvLOX10, and AtLOX2 belong to the 13-LOX subfamily, indicating a possible functional similarity in those tissues. Notably, most FvLOX genes exhibit low expression levels in fruits, which is consistent with

findings in peaches, grapes, watermelons, and tomatoes. The reduced expression of the LOX gene in these fruits suggests that plants might require LOX activity for cell division and fruit growth during early developmental stages. Previous studies have shown that AtLOX1 is significantly expressed under ABA treatment. It was observed that FvLOX4 was up-regulated by 15.92 times when treated with ABA, and both FvLOX4 and AtLOX1 are part of the 9-LOX subgroup, indicating they may have comparable functions. Additionally, FvLOX3 also shows increased expression in response to drought stress; however, there is limited literature on this subject and insufficient information for further elaboration (LI *et al*., 2022).

FvSTOP1

It is a protein localized in the nucleus that exhibits self-activation characteristics and shows peak expression in both ripening fruit and roots. The stable overexpression and deletion of FvSTOP1 in woodland strawberries resulted in increased and decreased anthocyanin levels in the fruit, respectively. FvSTOP1 promotes anthocyanin accumulation by activating the expression of glutathione S-transferase FvTT19. Notably, FvSTOP1 was found to interact with the strawberry anthocyanin repressor FvMYB1, although it did not alter the protein levels of FvMYB1. Additionally, FvSTOP1 interacted with the strawberry anthocyanin activator FvbHLH33, leading to the formation of a complex consisting of FvSTOP1, FvMYB1, and FvbHLH33. FvSTOP1 mitigated the repression exerted by the FvMYB1–FvbHLH33 complex on the expression of FvTT19, FvCHS, and FvF3H by preventing the formation of this repression complex, thus facilitating anthocyanin accumulation. The levels of genes associated with anthocyanin biosynthesis and transport were notably heightened in the fruits of FvSTOP1 overexpressing plants, while they were significantly reduced in knockout plants (Fig. 3). Its distinctive regulatory function in anthocyanin biosynthesis, along with its similarity to stress-related STOP1, positions it as a valuable target for enhancing fruit quality and stress tolerance (Bian *et al*., 2025).

FveIPT2

Anthocyanins, the main pigments found in strawberries, along with terpenoids important secondary metabolites in plants play a significant role in enhancing fruit quality and nutritional value. These secondary metabolites are widely recognized for their numerous health advantages (Tang *et al*., 2024). Research has indicated that cytokinins (CK) can promote the accumulation of anthocyanins in various plant species such as Arabidopsis, apple, strawberry, and Eucalyptus, while also regulating the biosynthesis of terpenoids in *Artemisia alba* and *Thymus vulgaris*. Considering the health benefits associated with anthocyanins and terpenoids, a previous study investigated whether manipulating a housekeeping IPT gene could boost the production of these compounds. In *Fragaria vesca*, the genes FveIPT2 and FveIPT7 are identified as part of the tRNA-type IPT family, while five other genes FveIPT1 and FveIPT3–6 are categorized as ATP/ADP-type IPTs (Mi *et al*., 2017). To further understand the function of tRNA-type IPTs in fruit quality, they overexpressed FveIPT2 in woodland strawberries. Unexpectedly, the overexpression of FveIPT2 had little effect on CK levels. However, it resulted in a notable increase in the concentrations of terpenoids and anthocyanins, which are secondary metabolites linked to fruit quality and coloration. These results provide experimental validation for the involvement of tRNA-type IPT genes and enhance our understanding of the regulatory mechanisms governing secondary metabolite synthesis in strawberries. This research emphasizes the housekeeping function of the tRNA-type IPT gene FveIPT2 and illustrates that its overexpression improves strawberry fruit quality without adversely affecting growth. The metabolic enhancements, facilitated through the upregulation of anthocyanin and terpenoid pathways, position FveIPT2 as a promising candidate for the genetic enhancement of strawberry fruit quality by increasing beneficial secondary metabolites. Additional studies are required to clarify the molecular mechanisms involved (Gan *et al*., 2025) (Han *et al*., 2024) (Fig. 2).

Gene editing

Genome editing is starting to make progress in more complex polyploid crops, such as the allo-octoploid strawberry. It has already been effectively utilized to alter several strawberry genes related to anthocyanin levels, fruit firmness, and resilience against post-harvest diseases. With the help of these genome assemblies, CRISPR/Cas genome editing is being increasingly employed to investigate and enhance important traits in strawberries. Additionally, methods like RNA interference, as well as stable or transient overexpression of transgenes, have been used to confirm gene function and assist in the identification of potential candidate genes.(Vondracek *et al*., 2024) Combining traditional breeding methods with CRISPR gene editing holds the promise of speeding up crop enhancement and enabling the development of high-quality plant varieties through precise breeding

techniques. The swift advancement of CRISPR/Cas-based gene editing technology presents fresh opportunities for improving crops (Chen *et al*., 2024). Various gene editing strategies have been documented for Rosaceae crops, including apple, grapevine, pear, and raspberry. In strawberries, gene editing has been employed to alter auxin biosynthesis genes (tryptophan aminotransferase of Arabidopsis 1 and auxin response factor 8) in *Fragaria vesca*, as well as fruit and plant development-related genes such as Tomato MADS box gene 6 (FaMADS6), phytoene desaturase (PDS), and Reduced Anthocyanins in Petioles (RAP) in F. × ananassa. The CRISPR/Cas9-induced mutation of the RAP gene resulted in changes to fruit color in both wild and cultivated strawberries. In a prior investigation, it was shown that CRISPR/Cas9 can effectively produce biallelic mutants at a high rate within the genomes of both diploid and octoploid strawberries (Wilson *et al*., 2019). The full octoploid strawberry genome sequence offers a record of the genes that could influence significant agricultural characteristics.(Folta & Barbey, 2019) Implementing CRISPR gene editing in octoploid strawberries necessitates careful procedures for tissue culture and plant regeneration (Kim *et al*., 2025).

Conclusion

The strawberry, a member of the Rosaceae family, is a popular and nutrient-dense berry that is cherished for its taste, fragrance, and bright red hue. Its widespread prominence is reflected in various uses, from being eaten fresh to being included in a variety of processed products such as jams and ice cream. Strawberries serve as critical sources of nutrients including protein, calcium, potassium, iron, vitamin C, fiber, and a range of phytochemicals and antioxidants. The phenolic compounds present in berries are linked to numerous potential health benefits, including anticancer, antioxidant, anti-inflammatory, and regulatory effects on cellular functions. The anticancer effects occur through mechanisms such as safeguarding DNA and influencing gene expression related to cell proliferation and programmed cell death (apoptosis). The primary method for propagating strawberries is through runners, which ensures that the new plants are genetically identical to the parent. Strawberry cultivation encounters considerable challenges from both biotic and abiotic stressors. Soil pathogens, such as those responsible for red stele (*Phytophthora fragariae*) and Verticillium wilt, pose threats, alongside a complex of organisms that cause black root rot. Diseases affecting leaves, including leaf blight, Ramularia leaf spot, and leaf scorch, are also common, with Angular leaf spot and various forms of Anthracnose emerging as increasingly pressing global concerns. Environmental stressors such as cold, heat, drought, and salt detrimentally influence strawberry growth, nutrient absorption, and ultimately, yield. Boosting the plant's resilience to these conditions is an important aim for breeders. Genes within the SWEET Gene Family, which are bidirectional sugar transporters, play a crucial role in plant growth, development, and responses to stress. Understanding these genes is essential for improving fruit quality, as their expression influences sugar accumulation. Research into LOX Gene Family genes is ongoing to uncover their regulatory potential in dealing with different abiotic stresses including temperature fluctuations, drought, and salinity. The FvSTOP1 protein manages the buildup of anthocyanins (the primary red pigments) by interacting with significant activators and repressors, making it an important target for improving fruit quality and stress resistance. The overexpression of the FveIPT2 gene, part of the tRNA-type IPT family, has been found to elevate the levels of beneficial secondary metabolites such as terpenoids and anthocyanins, enhancing fruit quality without negatively impacting growth. State-of-the-art techniques like CRISPR/Cas gene editing are being applied more frequently to explore and improve significant traits such as anthocyanin levels, fruit firmness, and resistance to diseases, paving the way for accelerated crop enhancement, even in complex polyploid crops like the allo-octoploid strawberry.

Future Perspectives

By employing reverse genetics methods (such as CRISPR/Cas9 knockout or RNA interference (RNAi) silencing), we aim to specifically diminish the expression of potential target genes like FanSWEET14 and FanSWEET15a in cultivated strawberries.

i. We hypothesize that silencing these genes will hinder sugar export, resulting in a notable increase in the total soluble sugar (TSS) content of the ripe berries. This would confirm their status as viable targets for enhancing quality.

ii. Future research should aim to explore the intricate regulatory framework that governs anthocyanin production in strawberries, placing special emphasis on linking important structural and regulatory genes with the LOX gene family to better understand its influence on fruit color and quality.

iii. Moreover, gene editing technologies may be utilized to investigate the functional significance of FveIPT2 genes that influence essential mechanisms and cytokinin levels impacting fruit

size, development, and resilience to stress. This has the potential to enhance nutritional quality and increase yield for the benefit of agriculture.

iv. Additionally, the signaling pathways related to pH and stress responses mediated by STOP1 could interact with anthocyanin biosynthesis in strawberries, necessitating an in-depth examination to elucidate its possible regulatory function and the associated pathways.

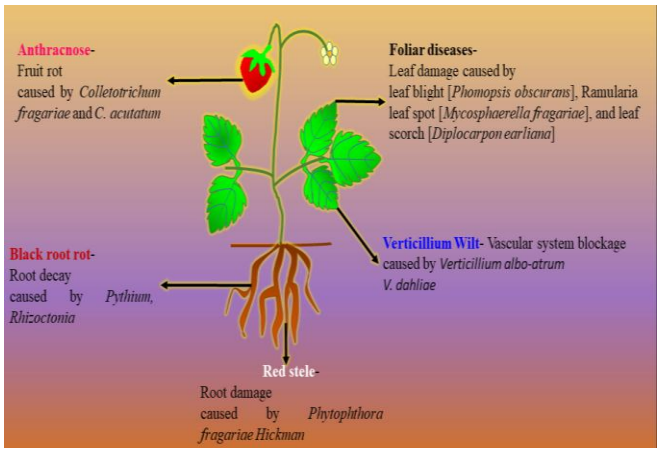

Fig. 1 : Biotic stressors affecting strawberry plant health (Palei *et al*., 2015)

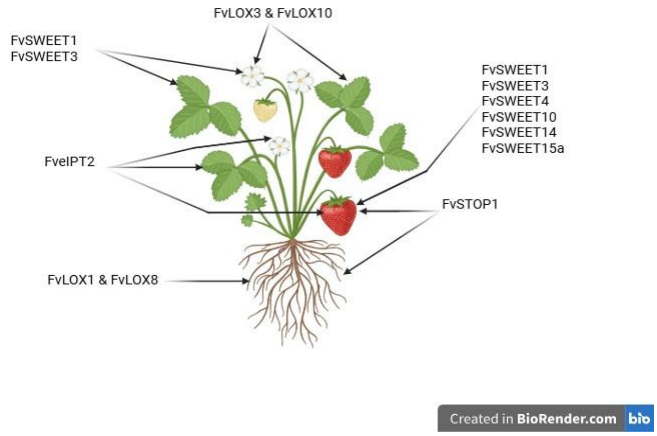

Fig. 2 : Tissue-specific expression of *FvLOX*, *FvSTOP1*, *FvSWEET*, and *FveIPT2* genes in *Fragaria vesca.* (LI *et al*., 2022) (Mi *et al*., 2017) (Bian *et al*., 2025) (Du *et al*., 2024)

The illustration highlights the expression patterns of important genes related to lipid oxidation, transcriptional regulation, sugar transport, and cytokinin biosynthesis in woodland strawberry. Transcripts of FvLOX1 and FvLOX8 are primarily found in the roots, while FvLOX3 and FvLOX10 exhibit high levels of expression in leaves and flowers. The FvSTOP1 protein is located in the nucleus and shows peak expression in ripening fruits and root tissues. Various members of the FvSWEET family demonstrate distinct tissue specificity: FvSWEET1 and FvSWEET3 are present in both flowers and leaves, whereas FvSWEET1, FvSWEET3, FvSWEET4, FvSWEET10, FvSWEET14, and FvSWEET15a have strong expression in fruits. Furthermore, FveIPT2—a gene associated with cytokinin biosynthesis—exhibits expression in leaves, flowers, and fruit tissues.

Competing Interests

The authors have no relevant financial or non-financial interests to disclose.

Data Availability declaration

No datasets were generated or analyzed in this study.

Author's Contribution

All authors contributed to the study conception and design. The first draft of the manuscript was written by Ritika Sharma and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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