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THE SILVER LINING OF STRESS: UNLOCKING THE POTENTIAL OF EUSTRESS IN VEGETABLE CROPS

Anushma P.* and T. Pradeepkumar

Department of Vegetable Science, College of Agriculture, Vellanikkara, Thrissur, Kerala – 680656, India

*Corresponding author E-mail: anushma922@gmail.com

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ABSTRACT

Climate change and rising food demand are intensifying pressure on vegetable production systems, which are highly vulnerable to both abiotic and biotic stresses. Stress, traditionally viewed as harmful, can be beneficial when applied in controlled doses, a phenomenon known as eustress. Mild stressors can be harnessed to improve resilience, productivity, and nutritional quality in vegetable crops. Evidence demonstrates that a diverse array of eustressors, including microbial inoculants, molecular elicitors, controlled temperature shifts, regulated irrigation, UV and visible light treatments, mechanical and electromagnetic stimuli activate physiological and molecular pathways such as reactive oxygen and nitrogen signalling, ion fluxes, and phytohormonal crosstalk. These responses often enhance antioxidant accumulation, improve flavour, extend postharvest quality, and confer cross-tolerance to multiple stresses. The concept of stress memory is emerging as a potential tool for crop breeding and management, offering sustainable, non-GMO approaches to enhance resilience. Although results from controlled studies are promising, challenges remain in optimizing stress type, timing, and intensity across species and environments. Integrating mechanistic understanding with agronomic strategies positions eustress-based interventions as a practical and climate-smart approach to strengthening vegetable production and supporting food security.

***Keywords* :** Priming, vegetables, crop resilience, phytochemicals, stress memory .

Introduction

In an era marked by accelerating climate change, resource depletion, and the need to feed a growing global population, enhancing the resilience and productivity of crops has become a central challenge in agricultural science (FAO, 2021). To keep pace with a global population expected to reach 10 billion by 2050, it is estimated that worldwide food production will need to expand by a significant 50–70% (Vos & Bellù, 2019). Instead of solely focusing on increasing production, reducing crop losses offers another solution, and the main factors contributing to these losses are abiotic and biotic stresses, which are predicted to become more intense due to climate change.

Traditionally, plant stress has been viewed predominantly through a negative lens associated with abiotic factors like drought, salinity, and temperature extremes, or biotic threats such as pathogens and herbivores, that impair growth, reduce yields, and compromise crop quality (Boyer, 1982; Mittler, 2006). Yet, over the past few decades, research has revealed a more nuanced view that not all stress exerts purely negative effects. Under controlled or moderate exposure, certain stress signals can stimulate adaptive responses that prove advantageous to the plant. This phenomenon, commonly referred to as *eustress*, reframes the discussion in plant science by emphasizing that stress, when appropriately managed, may in fact support resilience and productivity rather than diminish them (Kranner *et al.*, 2010; Calabrese & Mattson, 2017).

Eustress, originally defined by endocrinologist Hans Selye during 1975 in animal physiology to describe stress that elicits positive biological outcomes. Its application to plants has gained traction more recently, especially with evidence showing that mild, transient stimuli can activate defense pathways, prime metabolic functions, and bolster tolerance to subsequent stress events (Conrath, 2006; Bruce *et al.*, 2007). Vegetable crops, known for their short life cycles, wide range of morpho-physiological features, and great metabolic adaptability, are quite sensitive to these kinds of priming stimuli. Additionally, since vegetables are consumed for their nutritional and phytochemical qualities, eustress-induced amplification of compounds like antioxidants, vitamins, and flavonoids offers dual benefits by not only strengthens their stress tolerance but also enhances their nutritional value (Dumitru *et al.*, 2023). Brief droughts or controlled exposure to salinity during vegetative growth, for example, have been demonstrated to enhance the phytonutrient content and antioxidant capacity of leafy greens and fruiting vegetables (Rouphael *et al.*, 2012). Similarly, exposing lettuce to supplemental UV light has been shown to trigger stress responses that boost flavonoid levels (Tsormpatsidis *et al.*, 2008). The idea of eustress presents a viable approach to optimising yield-quality in the context of sustainable agriculture without depending on artificial inputs. Eustress-based techniques can be used as low-input, natural means of fortifying vegetable crops against changing weather patterns and satisfying consumer nutritional needs as the movement towards agroecological intensification gets momentum. Furthermore, such strategies align with consumer expectations for residue-free, nutrient-rich vegetables and contribute to reducing chemical footprints in production systems.

Despite its potential, eustress application remains an emerging frontier in vegetable science. The effectiveness of such approaches depends on species, developmental stage, environmental context, and stressor characteristics such as type, intensity, duration, and frequency. Over-application or poor timing might shift the equilibrium from eustress to distress, compromising plant health and productivity. This demands a mechanistic understanding of comprehension of the perception and transduction of specific stress signals within the plant, along with insights into dose-response relationships and metabolic trade-offs (Agathokleous *et al.*, 2019). In spite of a number of experimental studies highlight the promise of hormesis-based treatments, Standardised techniques for commercial-scale application are absent**.** This emphasises the necessity of conducting methodical, multidisciplinary research that combines postharvest biology, agronomy, omics technologies, and plant physiology. The main stressors, crop-specific reactions, and ways to use controlled abiotic stress as a tool to increase crop resilience, productivity, and quality in sustainable vegetable production systems are all covered in this review.

The Dichotomy of Stress

The core idea of eustress conceptually aligns with the principle of hormesis, a term originally derived from medical research on toxins administered at low doses. Hormesis refers to a biphasic response in which high concentrations of a substance are damaging, whereas low concentrations can induce beneficial effects. These positive outcomes typically result from a modest overcompensation by the organism, a process often described as "hormetic low-dose stimulation" (Agathokleous & Calabrese, 2024). Fundamentally, hormesis recognizes living organisms as dynamic and adaptable systems capable of turning limited stress exposure into an advantage for survival.

The inability of plants to escape environmental stresses makes hormetic principles relevant for understanding their adaptive responses. These stresses frequently occur in combination can affect the growth and overall productivity of plants substantially. Regulating these dynamic stresses represents a central evolutionary challenge for plants and is vital for revealing the limits of their adaptability (Raza *et al.*, 2020). To withstand the persistent stresses plants have evolved complex mechanisms to detect external cues (Fujita *et al.*, 2006). These signals trigger modifications in signalling molecules, gene transcription, non-coding RNAs, proteins, and metabolites in order to enhance plant's resilience (Long, 2011). While prolonged or severe stress is frequently harmful, mild stress can trigger adaptive processes that increase resilience. The ultimate effect of a stressor thus hinges on its strength and exposure time, allowing it to function beneficially or detrimentally.

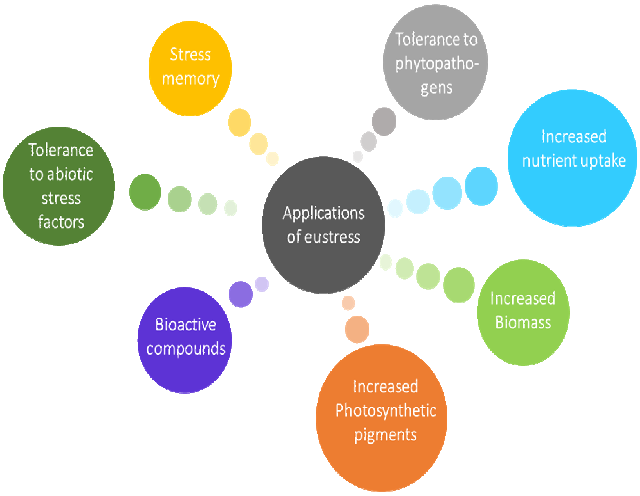

Fig.1: Different applications of eustress in vegetable crops

Mechanism of Eustress Perception and Response in Plants

Plants have developed intricate systems to detect, interpret, and retain stress-related information, forming the basis for adaptive responses that persist beyond the initial stress event.

Perception and Signalling of Eustress

The recognition of eustress relies on complex molecular systems that enable plants distinguish between harmful distress and beneficial eustressor stimuli (Vázquez-Hernández *et al.*, 2019). This discriminative ability is grounded in the plant's capacity to perceive external stimuli through specialized receptors and signalling cascades which in turn modify patterns of gene expression to generate molecular memory traces.

The initial perception of eustressors occurs at the cellular level through multiple recognition mechanisms including microbial -associated molecular patterns (MAMPs), damage-associated molecular patterns (DAMPs), and environmental signal transduction pathways. Detection of eustress prompts the plants to launch swift signalling events involving chloride, potassium, and calcium ion fluxes followed by the production of reactive oxygen and nitrogen species that function as secondary messengers. This cascade then initiates mitogen-activated protein kinases and engage hormone pathways involving salicylic acid, abscisic acid, and jasmonic acid, establishing a complex regulatory network that governs the cellular response (Pastor *et al.*, 2013).

Stress Memory

Stress memory represents a vital adaptive mechanism in plants, allowing them to anticipate recurring environmental pressures. By preserving information from previous stress events plants can fine tune their responses to subsequent stresses, responding more proficiently when confronted with familiar threats (Lämke and Bäurle, 2017; Galviz *et al.*, 2020). The plant memory system functions on several temporal levels ranging from short-term somatic memory that endures for days or weeks, to intergenerational memory spanning one or two stress-free generations extending to transgenerational memory that can persist across several generations (Crisp *et al.*, 2016).

Stress memory is initiated and preserved through epigenetic mechanisms, where DNA methylation, histone post-translational modifications (PTMs), and small RNAs (sRNAs) function as lasting molecular imprints that store stress-related information (Mirouze & Paszkowski, 2011). The precision of stress memory formation depends on the nature, intensity, and duration of the eustressor treatment, with recent evidence suggesting that memory creation is random and context-specific rather than consistent across all cases. (Crisp *et al.*, 2016). Experimental studies have demonstrated that treatments with β-aminobutyric acid (BABA) can induce heritable pathogen resistance in potato through general hypermethylation states and specific methylation changes in resistance gene promoters (Kuźnicki *et al.*, 2019). Similarly, hydrogen peroxide treatment has shown to alter methylation status at specific loci, leading to improved heat stress tolerance without compromising the overall plant phenotype (Cao *et al.*, 2013). These findings highlight the precision with which plants can encode beneficial stress experiences into their epigenetic landscape.

Correspondingly cross-tolerance represents an important aspect of eustress-induced memory, where exposure to one type of eustressor can enhance plant responses to different stress factors through overlaying signaling pathways (Lämke and Bäurle, 2017). This phenomenon is mediated by the activation of multiple signaling networks and the establishment of epigenetic marks associated with broad-spectrum stress responses. Moderate temperature treatments or salt exposure can induce enhanced immunity to bacterial pathogens, with these effects being associated with specific histone PTM marks including H3K14ac, H3K4me2, and H3K4me3 (Singh *et al.*, 2014).

Contemporary research has revealed that the perception of eustress and establishment of stress memory involve complex interactions between primary and secondary metabolism, with reactive oxygen-nitrogen-sulphur species playing crucial roles as signalling molecules and epigenetic modulators (Locato *et al.*, 2018; Saravana Kumar *et al.*, 2020). These metabolic intermediates not only serve as stress sensors but also directly govern the activity of enzymes involved in DNA methylation and histone modifications creating direct links between metabolic status and epigenetic regulation. This integration of metabolic and epigenetic signals enables plants to cipher environmentally relevant information into heritable molecular marks that can guide adaptive responses in future generations.

Interestingly, when plants perceive eustress they engage in subtle cost–benefit decisions that influence whether the experience is remembered for future responses or simply forgotten. During stress recovery periods, plants must balance the metabolic costs of maintaining defensive states against the potential benefits of enhanced preparedness for future stress events (Crisp *et al.*, 2016). This decision-making process occurs at the molecular level through trade-offs between growth and development resources and the establishment of protective memory states. When the benefits of memory exceed the costs, stable epigenetic marks are established that can persist across generations, while unfavourable conditions may lead to memory resetting and return to baseline states.

Classification of eustressors

Eustressors, both biotic and abiotic in nature are available. The former includes biological elicitors while physical and chemical eustressors are of non-biological origin. The agents promote plant performance by regulating physiological functions, hence greater productivity, quality output, longer postharvest life, and conservation (Vázquez-Hernández *et al.*, 2019).

Biotic eustressors

Plants constantly interact with a wide array of living organisms, including beneficial microbes, pathogens, and herbivores. Some of these biotic interactions act as eustressors, eliciting controlled stress responses that prime plants for enhanced growth, defense, and resilience under adverse environmental conditions.

Beneficial microbes

Beneficial microbes, particularly Plant Growth-Promoting Rhizobacteria (PGPR), enhance plant resilience to environmental stresses by inducing morphological and metabolic adjustments that lead to induced systemic tolerance. These rhizobacteria employ multiple mechanisms, including the production of ACC (1-aminocyclopropane-1-carboxylate) deaminase to limit stress-induced ethylene accumulation, modulation of phytohormone activity, stimulation of antioxidant enzymes, and improvement of nutrient uptake. They also mitigate abiotic stress by reducing the absorption of excess salts and heavy metals while activating stress-responsive genes, collectively supporting growth and tolerance under adverse conditions (Vurukonda *et al.*, 2016; Etesami & Maheshwari, 2018). The rhizobacterium *Bacillus amyloliquefaciens* TBorg1 enhanced tomato growth, suppressed Tobacco mosaic virus severity and accumulation, and activated systemic resistance through biochemical and molecular mechanisms, underscoring its potential as a sustainable biocontrol agent (Abdelkhalek *et al.*, 2022). Similarly, *Bacillus licheniformis* alleviated arsenic and cadmium toxicity in *Spinacia oleracea* L. by upregulating stress-responsive genes, increasing antioxidant enzyme activities (SOD, POD, CAT), and reducing oxidative damage, as indicated by lower MDA levels (Asif *et al.*, 2023).

Microbial-Associated Molecular Patterns

Microbe-Associated Molecular Patterns (MAMPs) are heterogenous compounds of fungal, bacterial, and nematode origin that serve as defence-elicitors in plants (Wiesel *et al.*, 2014). In fungi, key elicitors include chitin-cell wall fragments, mannoproteins, and β-glucans that induce numerous defence-eliciting responses. Bacterial elicitors include extracellular polysaccharides, lipopolysaccharides, flagellin, elongation factor Tu (EF-Tu), and several metabolites that seem to act individually or in concert (Dodds & Rathjen, 2010). Rajamanickam and Nakkeeran (2020) demonstrated that flagellin released by *Bacillus amyloliquefaciens* CRN9 triggered systemic defence in chilli and inhibited Groundnut bud necrosis virus replication. Recently, nematode-produced signalling molecules, known as Nematode-Associated Molecular Patterns (NAMPs) have been identified which act as pheromones recognized by plants and trigger innate immune responses, thereby enhancing resistance to a wide range of nematode and microbial pathogens (Goode & Mitchum 2022).

Damage-associated molecular patterns

Damage-Associated Molecular Patterns (DAMPs) represent a class of plant-derived elicitors that act as internal signals of tissue injury (Hou *et al.*, 2019). Released from damaged tissues, these molecules function as a warning system by activating immune responses in neighbouring cells. Typical DAMPs include fragments of cell wall components such as β-glucans, oligogalacturonides, and xylose, as well as phenylpropanoid-related metabolites and extracellular nucleotides (eATP, eDNA, and eNAD[P]), which are often generated following herbivore attack (Li *et al.*, 2020; Harris & Mou, 2024). In tomato, oligogalacturonides released from damaged cell walls, act as danger signals that primarily activate defense responses in the roots which leads to systemic immunity and increased resistance to pathogens like *Botrytis cinerea* (Gamir *et al.*, 2021).

Herbivore-associated molecular pattern

Overtime, plants have evolved intricate mechanisms to sense when they are under attack by herbivores. Insects release diverse chemical cues during feeding, including those contained in saliva, oral and oviposition secretions, and faecal matter, which plants recognize through specific receptor systems. Recognition of these signals triggers innate immune responses, including modifications to the cell wall and activation of defense pathways (Kloth *et al.*, 2019; Acevedo *et al.*, 2015). In addition to these direct responses, plants release volatile compounds in reaction to herbivore attack. These herbivore-induced volatiles act as warning signals, not only alerting other parts of the same plant but also priming neighbouring plants to respond more quickly and robustly if they are attacked subsequently (Kalske *et al.*, 2019; Mauch-Mani *et al.*, 2017). Tomato plants infested with spider mites release volatiles that reduce the susceptibility of nearby plants to whitefly-transmitted TYLCV by activating jasmonic acid–mediated defenses (Yang *et al.*, 2024). Similarly, the diamondback moth (*Plutella xylostella*) produces oral secretions containing a protein and a core peptide that act as HAMPs, stimulating abscisic acid accumulation in cruciferous plants and amplifying their resistance to insect feeding (Yun *et al.*, 2025).

Abiotic Eustressors

Stemming from non-living sources, abiotic eustressors can be categorized into physical and chemical types. Physical eustressors include factors such as light, temperature fluctuations, water availability, and mechanical stimuli, while chemical eustressors encompass elements like salinity, mineral nutrients, and low-dose reactive oxygen species. These mild stresses can stimulate adaptive responses in plants, enhancing their growth, metabolism, and stress tolerance without causing lasting damage (Vázquez-Hernández *et al.*, 2019).

Chemical eustressors

Salinity

Salinity is primarily regarded as a chemical stressor because, at high levels, it disrupts the uptake and balance of essential nutrients, impairing plant growth, while also producing an osmotic effect similar to that caused by drought (Shrivastava & Kumar, 2014). It affects both the physical attributes and chemical composition of many horticultural crops (Colla *et al.*, 2013). Vegetable crops differ in their tolerance to salinity. Broccoli, cabbage, cauliflower, cucumber, eggplant, lettuce, pepper, pumpkin, radish, tomato, and turnip are generally considered moderately sensitive. In contrast, red beet and asparagus show relatively higher tolerance, while carrot, okra, onion, and pea are among the most salt-sensitive vegetables (Shahbaz *et al.*, 2012). Applying moderate salinity in a controlled manner, by regulating the electrical conductivity and nutrient solution concentration, can enhance the production and accumulation of beneficial phytochemicals (Kyriacou & Rouphael, 2018). This type of mild stress, considered a form of eustress, activates targeted physiological and molecular mechanisms in plants, leading to the strategic accumulation of bioactive compounds that improve adaptation to less-than-optimal conditions. Studies have demonstrated that salinity eustress in vegetables can increase non-structural carbohydrates and key health-promoting compounds such as lycopene, β-carotene, vitamin C, and phenolics, while also reducing nitrate levels due to competitive interactions between chloride and nitrate ions for the same uptake channels (Rouphael & Kyriacou, 2018). Mild salinity can enhance certain stress-related metabolites in microgreens without compromising overall yield (Plocek *et al.*, 2023). Mild salinity eustress in hydroponic lettuce enhances bioactive compounds, improves plant resilience, and preserves post-harvest nutraceutical quality without reducing yield (Carillo *et al.*, 2021). Moderate salinity stress in red lettuce enhances phenolic compounds and antioxidant activity without reducing growth, improving its functional quality (Santander *et al.*, 2022). Although moderate salinity reduced cherry tomato yield but enhanced fruit quality by increasing sugars, proline, and total soluble solids without altering key organic acids (Agius *et al.*, 2022).

Nanostructures

Nanoparticles, with their distinctive features such as high surface area, mobility, reactivity, and diverse shapes, are increasingly viewed as innovative agents for promoting sustainability in agriculture (Javed *et al.*, 2022). These increases the accumulation of reactive oxygen species in the plant cell which triggers oxidative stress and changes in primary and secondary metabolites. The enzyme-linked immunosorbent assay showed a marked reduction in cucumber mosaic virus accumulation in cucumber plants treated with nickel oxide nanostructures compared to untreated plants (Derbalah & Elsharkawy, 2019). Zhuang *et al.* (2025) showed that seed priming with silica nanoparticles (40 mg/L, 4 h) in cucumber induces eustress that enhances germination, seedling vigour, root and shoot growth, increases levels of sugars, amino acids, antioxidants and signalling molecules, upregulates drought tolerance genes, and improves resilience even in the next generation, without compromising yield or fruit quality. Morales-Espinoza *et al.* (2019) reported that treatment with selenium (Se) nanoparticles improved tomato growth and boosted antioxidant activity when plants were exposed to salt stress. Chitosan-selenium (Cs–Se) nanoparticles strengthened bitter melon's tolerance to salt stress by enhancing enzymatic activity, increasing proline, relative water content, and potassium (K^+) levels, while reducing MDA, H_2O_2, and sodium accumulation in plant tissues

(Sheikhalipour *et al.*, 2021). Iron nanoparticles contribute to improved stress tolerance by promoting chlorophyll synthesis, achieved through the activation of protoporphyrin, magnesium protoporphyrin, and protochlorophyllide (Rezayian *et al.*, 2023).

Inorganic salts and elements

Inorganic salts of essential plant nutrients have been identified as possessing antifungal activity (Deliopoulos *et al.*, 2010). Compounds such as chlorides, phosphates, phosphites, silicates, and carbonates exhibit antimicrobial potential by modulating pH balance, redox status, osmotic regulation, phytohormone signalling, and enzymatic functions linked to stress adaptation (Chakraborty *et al.*, 2015). Oyarburo *et al.* (2015) showed that potassium phosphite pretreatment enhanced UV-B stress tolerance in potato by preserving chlorophyll, upregulating the psbA gene encoding the D1 protein of photosystem II, and reducing oxidative damage, indicating its role in mediating UV-B resilience. El-Nakhel *et al.* (2019) showed that controlled macronutrient deprivation in butterhead lettuce induces the accumulation of secondary metabolites, with cultivar-specific responses in red and green types, highlighting mild nutrient stress as a promising approach to enhance nutritional and functional quality in soilless systems.

Beneficial elements like aluminium, cobalt, sodium, selenium and silicon enhance plant defence against biotic and abiotic stress. These elements strengthen the cell wall, regulate osmotic balance and enzymatic activity, reduce transpiration and mitigate heavy metal toxicity thereby contributing to improved yield and stress tolerance (Pilon-Smits *et al.*, 2009; Zengin & Munzuroglu, 2005; Luciano *et al.*, 2017). Valencia-Hernandez *et al.* (2023) demonstrated that low, eustressic doses of cadmium primed tomato plants by enhancing antioxidant defenses and stress-related enzymes, which improved resistance against *Clavibacter michiganensis* infection. In China, rare elements such as lanthanides, scandium, and yttrium have gained research attention as studies have indicated that these elements at low concentration can enhance antioxidant enzyme activity, total phenolic content, and carotenoid levels thereby modulating enzymatic processes and stimulating secondary metabolism (Gopal & Rizvi, 2008; Emmanuel *et al.*, 2010). Lanthanides such as lanthanum can improve crop yield and fruit quality at low concentrations but may induce toxicity at higher levels (Agathokleous *et al.*, 2018). Wang *et al.* (2008) reported that rare earth elements altered the distribution of essential minerals and heavy metals in horseradish, indicating their role in modulating nutrient balance and stress responses.

Ozone

Although atmospheric ozone (O_3) is a major pollutant that can harm plant growth and development, recent studies suggest it may have agricultural benefits as a sustainable alternative to conventional agrochemicals. At low concentrations, O_3 can trigger plant defense responses and stimulate the production of secondary metabolites (Risoli & Lauria, 2022). Pastacaldi *et al.* (2025) found that ozone treatments can promote plant growth and activate defense mechanisms through salicylic acid signalling and pathogenesis-related proteins. However, their effectiveness depends on factors such as plant species, ozone concentration, and application method. In tomato, ozonated water increased resistance against *Meloidogyne incognita* and Tomato spotted wilt virus by activating salicylic acid–mediated defenses. The method of application influenced the outcome, soil drenching reduced nematode infection, while foliar spraying lowered viral incidence (Prigigallo *et al.*, 2019). In cucumber, irrigation with moderate levels of ozonated water (≈0.5–1 ppm) alleviated drought stress and improved fruit yield, vegetative growth, and quality traits compared to untreated plants (Najarian *et al.*, 2018). Similarly, in tomato, ozonated water enhanced plant growth, yield, and fruit nutritional quality by increasing antioxidants and ascorbic acid content (Tahamolkonan *et al.*, 2022).

Physical eustressors

Temperature

Plant growth and development are closely associated with the temperature conditions of their native environment. Exposure to temperatures beyond the optimal low or high range can adversely affect both growth and overall productivity. However, controlled exposure to temperature stress, known as thermopriming, can enhance plant resilience (Bäurle, 2016). Brief periods of low-temperature exposure can induce hardening, enabling tissues to better tolerate subsequent chilling stress with minimal damage (Miao *et al.*, 2009). Similarly, mild heat priming has been shown to improve crop tolerance to high temperatures. He *et al.* (2019) reported that mild heat priming enhanced root growth, photosynthesis, and yield in temperate vegetables grown under tropical conditions, while He *et al.* (2022) demonstrated that root-zone heat priming in aeroponically grown leafy greens improved PSII efficiency, root development, yield, and nutritional quality under tropical greenhouse conditions.

Thermopriming can also induce cross-tolerance, where exposure to mild heat stress enhances tolerance to other stresses. Tomato plants subjected to mild heat stress exhibited improved salinity tolerance through metabolic reprogramming, including osmolyte accumulation and enhanced antioxidant activity (Körner *et al.*, 2024). In greenhouse cultivation, manipulating suboptimal temperatures is a widely applied strategy to improve product quality. In tomato, such management has been linked to enhanced fruit attributes (Ntatsi *et al.*, 2014). At the physiological level, thermomorphogenic responses in tomato involve changes in gibberellin biosynthesis and tissue sensitivity. While thermopriming promotes the accumulation of antioxidative pigments during subsequent heat stress, temporary reductions in growth and chlorophyll content may occur. However, the benefits are typically more pronounced at the reproductive stage (Röhlen-Schmittgen *et al.*, 2022).

Deficit irrigation

While drought is a major abiotic stress that disrupts plant physiological and biochemical processes, limiting growth, development, and yield, carefully managed water deficits can have beneficial effects. Deficit irrigation is a water-management strategy that supplies less water than the full crop requirement with the goal of maintaining yield and quality. It can be applied as sustained deficit irrigation (SDI), where water is consistently restricted throughout the crop cycle or as regulated deficit irrigation (RDI), where water reduction is imposed only during growth stages when the crop is less sensitive to water stress (Chai *et al.*, 2014). In particular, deficit irrigation can improve fruit quality by increasing the accumulation of phytochemicals and flavour-related compounds in various crops. Liu *et al.* (2006) reported that applying mild RDI during early growth stages enhanced plant resilience to drought and preserved tolerance in later developmental stages. Similarly, Hachmann *et al.* (2019) demonstrated that moderate RDI not only maintained cauliflower yield but also enhanced its antioxidant activity and phenolic content.

Beyond improvements in fruit quality, RDI supports other important horticultural traits, including compact plant architecture, shorter internodes, uniform leaf development, and increased floral bud initiation. These responses are driven by multiple mechanisms like morphological adaptations such as a higher root-to-shoot ratio and improved nutrient uptake, physiological adjustments including stomatal regulation, reduced leaf respiration, and sustained photosynthesis; and biochemical modifications such as enhanced antioxidant enzyme activity and increased production of signalling molecules (Chai *et al.*, 2016).

UV Irradiation

Ultraviolet (UV) radiation is often considered detrimental to plants because it disrupts photosystem II by damaging essential components such as the Mn_4CaO_5 cluster (Khudyakova *et al.*, 2019). Based on wavelength, solar UV radiation is classified into three groups: UV-A (320–400 nm), UV-B (280–320 nm), and UV-C (100–280 nm). The stratospheric ozone layer effectively blocks UV-C and most UV-B radiation allowing only UV-A and a small fraction of UV-B to reach the Earth's surface. Although UV-B represents just 0.5–0.7% of total solar energy, its high energy makes it particularly damaging to living organisms, including plants.

Despite its negative reputation, research has shown that UV radiation can also serve as a eustress factor, influencing plant growth, photosynthesis, secondary metabolite accumulation, and even plant–pest interactions. In greenhouse settings, UV exposure has been reported to disrupt pathogen life cycles, alter insect behavior, and strengthen plant defense responses (Raviv & Antignus, 2004). Specifically, UV-C has been employed successfully in postharvest treatments, where it not only disinfects fruit surfaces but also enhances disease resistance (Vàsquez *et al.*, 2017). Charles *et al.* (2008) demonstrated that postharvest UV-C treatment of tomato fruit enhanced resistance to *Botrytis cinerea* by promoting lignin and phenolic deposition. Qian *et al.* (2020) reported that UV-A exposure induced compact, dwarf growth in cucumber without reducing fruit yield, suggesting its usefulness in improving plant architecture. Escobar-Hernández *et al.* (2024) further showed that UV-A seedling priming enhanced growth, chlorophyll content, and antioxidant defenses in tomato and bell pepper under water stress, thereby improving drought resilience. Similarly, Liu *et al.* (2025) found that short-term postharvest exposure to UV-A and UV-B increased the accumulation of bioactive compounds, carotenoids, and antioxidants in leafy vegetables, enhancing their nutritional quality.

Acoustic vibrations

Sound is a mechanical stimulus that travels as waves through different media, carrying energy and information (Jung *et al.*, 2018). Plants, as highly responsive organisms, can both produce and perceive these acoustic signals from their environment (Mishra *et al.*, 2016). Sounds generated by stressed plants, herbivores, water, or pollinators enable plants to anticipate potential threats. In response, plants enter a primed state that alters their metabolic, hormonal, and biochemical pathways and can also trigger epigenetic changes to enhance stress preparedness. Exposure to sound has been shown to activate plant innate immunity by initiating salicylic acid and jasmonic acid signalling pathways, responses that closely resemble those induced by chemical elicitors (Ghosh *et al.*, 2016). Sound treatments can additionally modify cell membrane structure, facilitating the movement of signalling molecules critical for defense (Mishra *et al.*, 2016). Among sounds beyond human hearing, ultrasounds exert the strongest effects on plants. Acting as an abiotic stressor, ultrasound produces a mechano-priming effect that stimulates stress-related defense mechanisms (Pesti-Asbóth *et al.*, 2022). For instance, in tomato, exposure to aerial ultrasound at 40.5 kHz enhanced resistance to *Fusarium oxysporum* by upregulating PR1a expression and activating salicylic acid–mediated defense pathways (Kawakami *et al.*, 2019). Similarly, ultrasound seed priming improved drought tolerance in pepper by increasing melatonin levels and antioxidant activity, thereby reducing oxidative stress (Yakupoğlu, 2023). In potato, ultrasound exposure has been found to modulate gene expression in *in vitro* plantlets. Dobránszki *et al.* (2019) demonstrated that exposing potato plantlets at different developmental stages alters mRNA transcription profiles, affecting growth and stress-related pathways. Likewise, Teixeira da Silva *et al.* (2020) found that piezoelectric ultrasound triggers transcriptomic changes in potato, triggering molecular mechanisms involved in stress responses and defense.

Visible light and LEDs

Beyond its fundamental role in photosynthesis, visible light has emerged as a powerful tool in modern horticulture, particularly through innovations in light-emitting diode (LED) technologies. These innovations have expanded the use of LEDs across greenhouses, vertical farms, growth chambers, and plant factories, where spectrum and intensity can be precisely tailored to production goals. Such spectral manipulations not only influence yield but also nutritional value, phytochemical accumulation, flowering dynamics, transplant success, and pre- and postharvest performance (Rahman *et al.*, 2021). In vertical farming, Nájera *et al.* (2022) demonstrated that optimizing light spectra, especially blue and red/far-red wavelengths enhanced vegetable productivity and nutritional quality by stimulating the accumulation of bioactive compounds such as antioxidants, phenolics, and sugars. At the postharvest stage, Hasperué *et al.* (2016) reported that white-blue LED illumination delayed senescence, preserved greenness, and boosted antioxidant and flavonoid content in Brussels sprouts, thereby extending shelf life. Similarly, targeted spectral combinations have proven effective for leafy greens and herbs. Naznin *et al.* (2019) reported that supplementing red LEDs with blue light improved growth, pigment synthesis, and antioxidant capacity in lettuce, spinach, kale, basil, and sweet pepper. When strategically managed visible spectra can elicit adaptive responses that simultaneously improve productivity and quality while offering sustainable opportunities for controlled-environment crop production.

Thigmomorphogenesis

The term originates from the Greek words *thigmo* and *morphogenesis* which means to touch and creation of form respectively. It describes the morphological changes that plants exhibit in response to physical contact or mechanical stimuli (Jaffe, 1973). As an adaptive strategy, it enables plants to combat mechanical forces encountered in natural ecosystems, including wind, rainfall, interactions with neighbouring vegetation, and herbivore activity, all of which can induce structural modifications (Biddington, 1986). These responses are typically manifested as reduced leaf area, petiole length, and overall height, coupled with thicker stem and altered root architecture. Collectively, these adjustments enhance mechanical stability and improved stress resilience (Braam, 2005). In tomato, rubbing of the internodes stimulates lignin-synthesizing enzymes, leading to stronger stem lignification and improved tolerance to mechanical stress (Saidi *et al.*, 2009). Castro-Estrada *et al.* (2025) reported that early mechanical stress in tomato not only promotes stem thickening and vascular development but also accelerates flowering and increases yield.

Electromagnetic stimulation

Exposure to electric and magnetic fields, as well as electric currents, can significantly influence plant growth, development, and metabolite production. Magnetic fields have been reported to improve plant stress tolerance by enhancing antioxidant levels and reducing oxidative damage (Radhakrishnan, 2019). In broad bean seedlings, low-intensity magnetic fields (10–100 μT at 50 Hz) modified membrane transport processes in root tips and facilitated the uptake of amino acids such as alanine (Stange *et al.*, 2002). Treatments with electric currents have been reported to accelerate germination and increase fresh biomass accumulation in leaves and roots of pea and broad bean, suggesting potential for improving productivity (Maffei, 2014). Similarly, weak pulsed electromagnetic field exposure of potato tubers not only elevated yield but also improved storage quality by lowering scab incidence and reducing postharvest weight loss (Bondarchuk *et al.*, 2023). Application of a magnetic field of 0.3 T to pepper seeds strengthened their tolerance to water-deficit conditions through melatonin-mediated activation of antioxidant defense system (Yakupoğlu, 2023).

Table 1 : Effect of different eustressors in vegetable crops

Eustressor	Crop	Effect	References
Salinity	*Solanum lycopersicum*	Increased lycopene, ascorbic acid, total phenolics content, and total antioxidant activity	Moya *et al.* (2017)
	Lactuca sativa	High Sugar, anthocyanin, chlorophylls and carotenoids	Sakamoto *et al.* (2014)
	Amaranthus gangeticus	Increased nutrients and phytochemicals	Sarker & Ercisli (2022)
Ozone	*Solanum lycopersicum*	Reduced nematode infestation	Veronico *et al.* (2017)
	Solanum lycopersicum	Enhanced photosynthesis, antioxidant enzyme activity and activated defense-related genes.	Xu *et al.* (2021)
Temperature	*Lactuca sativa*	Enhanced productivity and photosynthetic performance	He *et al.* (2022)
Deficit irrigation	*Solanum lycopersicum var. cerasiforme*	Higher content of soluble sugars, carotenoids, and total phenols	Coyago-Cruz *et al.* (2019)
	Cucumis sativus	Improved growth, physiology, and yields	Parkash *et al.* (2021)
UV-A	*Solanum lycopersicum*	Higher number of fruits, maturation synchronization and increased phenolic compounds	da Ponte (2017)
	Solanum lycopersicum	Increased PSII peptides and ribulose bisphosphatecarboxylase/oxygenase (Rubisco) transcription	Mariz-Ponte *et al.* (2021)
	Spinacia oleracea	Enhanced growth, total phenols, flavonoids and antioxidants	Choi *et al.* (2024)
UV-B	*Spinacia oleracea*	Enhanced chlorophyll and mineral retention	Kibar & Kibar (2025)
UV-C	*Lactuca sativa*	Enhanced plant performance and resistance to *Xanthomonas campestris* pv. *vitians*.	Sidibé *et al.* (2022)
Blue light	*Capsicum annuum*	High capsacinoids	Yap *et al.* (2021)
Red light	*Capsicum annuum*	High capsacinoids, stem elongation, leaf expansion, and increased photosynthesis	Gangadhar *et al.* (2012)
Red and blue light	*Capsicum annuum*	Increased Carotenoids, total phenols, vitamin C and antioxidant capacity	Pola *et al.* (2019)
Thigmomorphogenesis	*Solanum lycopersicum*	Increased leaf net CO_2 assimilation rates, reduced height, increased nitrogen content	Sparke *et al.* (2021)
	Lactuca sativa	Modified root architecture and increased metabolite synthesis	Baiyin *et al.* (2023)
Ultrasound	*Solanum tuberosum*	Increased total and marketable tuber yield	Pszczółkowski & Sawicka (2023)
	Cucumis sativus	Accelerated seed germination and flowering	Koochani *et al.* (2020)
	Solanum lycopersicum	Increased growth and yield parameters	Jamshidi *et al.* (2019)
Acoustic vibration	*Lactuca sativa*	Improved nutrient and water absorption, enhanced vegetative growth	Hendrawan *et al.* (2020)
	Cucumis sativus, *Solanum lycopersicum,* *Capsicum annuum*	Increased yield and reduced incidence of pest	Hou *et al.* (2009)
	Spinacia oleracea	Enhanced plant height, leaf area and chlorophyll content	Hendrawan *et al.* (2025)

Conclusions

The strategic application of eustressors offers a promising pathway to enhance crop resilience, productivity and nutritional quality in vegetables amid climate change and increasing global food demand. Mild stress treatments activate physiological, biochemical and molecular mechanisms that strengthens plant tolerance to biotic and abiotic challenges. These adaptive responses contribute to desirable outcomes such as elevated levels of bioactive compounds, improved flavour, enhanced postharvest quality and robust growth. To unlock the full potential of eustress, future research should identify the most effective stressors, optimal timing, dosage and stage of application that maximize benefits without compromising yield.

The key advantages of this approach lie in its efficiency and sustainability. Eustressors offer a cost-effective method that often doesn't require any specialized equipment. Exploring the impacts of combined or sequential eustress applications could also provide valuable insights into synergistic or antagonistic interactions reflecting real world conditions. Such investigations may pave the way for inducing broad spectrum stress. Equally important is the evaluation of these approaches across diverse climates and cultivation systems to ensure broad applicability and reliability. Large-scale field trials are necessary to confirm results from controlled environments and assess their practical feasibility in commercial production. Incorporating eustress-induced stress memory into breeding and crop management could provide a sustainable, non-GMO pathway to improve vegetable resilience. By harnessing natural plant defense, eustress-based strategies can accelerate the development of stress-resilient varieties contributing to global food security. Further research into the mechanisms and applications of eustress will be essential for building a more robust and sustainable agricultural system for the future.

Abbreviations

MAMPs	Microbial -associated molecular patterns
DAMPs	Damage-associated molecular patterns
HAMPs	Herbivore-associated molecular patterns
NAMPs	Nematode- associated molecular patterns
PTMs	Post-translational modifications
sRNAs	Small RNAs
BABA	β-aminobutyric acid
PGPR	Plant Growth-Promoting Rhizobacteria
ACC	1-aminocyclopropane-1-carboxylate
SOD	Super oxide dismutase
POD	Peroxidase
CAT	Catalase
TYLCV	Tomato yellow leaf curl virus
MDA	Malondialdehyde
eATP	Extracellular Adenosine Triphosphate
eDNA	Environmental DNA.
eNAD(P)	Extracellular Nicotinamide Adenine Dinucleotide (Phosphate)
GMO	Genetically modified organism

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