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Review

γ Aminobutyric Acid (GABA): A Key Player in Alleviating Abiotic Stress Resistance in Horticultural Crops: Current Insights and Future Directions

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Citation: Hayat, F.; Khan, U.; Li, J.; Ahmed, N.; Khanum, F.; Iqbal, S.; Altaf, M.A.; Ahmad, J.; Javed, H.U.; Peng, Y.; et al. γ Aminobutyric Acid (GABA): A Key Player in Alleviating Abiotic Stress Resistance in Horticultural Crops: Current Insights and Future Directions. *Horticulturae* **2023**, *9*, 647. https://doi.org/10.3390/horticulturae9060647

Academic Editors: Daniela Romano and Stefania Toscano

Received: 4 May 2023
Revised: 24 May 2023
Accepted: 29 May 2023
Published: 31 May 2023

Abstract: Gamma-aminobutyric acid (GABA) is a non-protein amino acid known for its role in the nervous system of animals. However, research has also revealed its presence and function in plants recently. In plants, GABA is a signal molecule involved in multiple physiological processes, including stress response, growth, and development. This review aims to present a thorough summary of the current knowledge regarding the role of GABA in plants. We begin by discussing the biosynthesis and transport of GABA in plants, followed by a detailed examination of its signaling mechanisms. Additionally, we explore GABA's potential roles in various plant physiological processes, such as abiotic stress response, and its potential application in horticultural plants. Finally, we highlight current challenges and future directions for research in this area. Overall, this review offers a comprehensive understanding of the significance of GABA in plants and its potential implications for plant physiology and crop improvement.

Keywords: GABA; abiotic stress; ROS; antioxidants; tolerance; plants; horticulture

1. Introduction

Under current climate change scenarios, there is an imperative need for collaborative research to develop crops that can withstand environmental challenges [1–3]. Environmental stresses, including heat, cold, salt, drought, and heavy metals, affect plant growth and development negatively, leading to significant declines in yield and quality [4–7]. However, studies have shown that GABA provides partial protection against abiotic stress in most plants [8,9]. Additionally, it has been found that gamma-aminobutyric acid (GABA) can improve plant growth and mitigate the adverse effects of stress by boosting antioxidant defense mechanisms, thereby enhancing plant stress tolerance. Using exogenous GABA enhances the activity of antioxidant enzymes and the glyoxalase system, crucial in detoxifying methylglyoxal [10]. The objective of this review was to gather and present various scientific studies that explore the function and mechanisms of GABA in horticultural plants when exposed to multiple environmental stresses.

GABA is a four-carbon molecule found in various organisms, including autotrophs and heterotrophs [11]. The first evidence of GABA was discovered in potato tubers, and it has since been found in plants, animals, and microbial organisms [12,13]. The GABA shunt pathway is responsible for synthesizing GABA, a non-proteinogenic amino acid, by the decarboxylation of glutamate and decarboxylation of glutamate with glutamate decarboxylase. GABA can also be obtained from polyamines, such as spermidine and putrescine, through the catalytic action of diamine oxidase and polyamine oxidase. The catabolism of GABA directly leads to succinic semialdehyde, which, in turn, transforms into succinate or hydroxybutyrate [14].

GABA is a natural active substance that plays a crucial role in various physiological activities of plants, such as growth, development, signaling, and stress responses [15–17]. Exogenous supplementation with GABA has been shown to stimulate plant growth. Moreover, this is achieved by enhancing endogenous GABA, amino acids, and hormone levels through upregulating crucial genes involved in phytohormones [18,19]. Studies have demonstrated that GABA can provide greater stress resistance in plants by regulating the expression of genes related to signaling, hormone biosynthesis, transcriptional regulation, the production of reactive oxygen species, and polyamine metabolism [20]. Furthermore, GABA plays a vital role in modulating the antioxidant system during plant growth and the transcription of genes that encode antioxidant enzymes, thereby mitigating plant oxidative damage [21]. The application of GABA is also significant in respiratory metabolism and changes the activity of many enzymes from the tricarboxylic acid (TCA) cycle [22]. Moreover, some studies also reported changes in the chlorophyll synthesis process due to exogenous GABA [23,24]. When exposed to salt stress, GABA can function as a non-toxic osmolyte and remove ROS to increase stress tolerance [25]. GABA not only regulates the osmotic balance in plants but has also been found to impact the accumulation of H_2O_2 and the ascorbic acid–glutathione cycle; as a result, the tolerance of muskmelon seedlings to saline–alkali stress is improved [26]. Another study reported that the exogenous GABA inhibits H_2O_2 production and controls H_2O_2-producing enzyme gene expression in Caragana intermedia under salt stress [27].

In summary, understanding the function of GABA in aiding horticultural plants to withstand abiotic stress is critical for ensuring the sustainable production of high-quality crops in an ever-challenging environment. This review provides an overview of the existing knowledge of and research advancements in GABA-triggered stress responses and their potential applications in managing horticultural plants. However, it is imperative to conduct further investigations into the underlying molecular mechanisms and signaling pathways to enhance crop resilience, optimize agricultural methods, and ultimately promote worldwide food security.

2. GABA Biosynthesis and Catabolism in Plants

Glutamate decarboxylase (GAD) catalyzes the synthesis of GABA from glutamate (Figure 1). GAD expression is regulated by various factors, including stress, and is encoded by multiple genes [28]. GABA can be catabolized by the enzyme GABA transaminase (GABA-T) into succinic semialdehyde, which is further metabolized into succinate through the activity of succinic semialdehyde dehydrogenase [29]. The tight regulation of GABA metabolism is essential for maintaining appropriate GABA levels within cells. Several plant species, such as Arabidopsis, tomatoes, grapevines, and apples, have shown increased GABA levels under drought stress. The upregulation of GABA biosynthesis in response to drought stress suggests that it may play a role in plant drought stress responses. GABA metabolism also depends on its transport. The activity of GABA-T, the enzyme responsible for GABA catabolism, is regulated by the intracellular GABA concentration. The transport of GABA can affect its intracellular concentration and, therefore, the activity of GABA-T [29]. Furthermore, the transport of GABA can affect the signaling pathways mediated by GABA, consequently affecting both plant growth and stress responses [30].

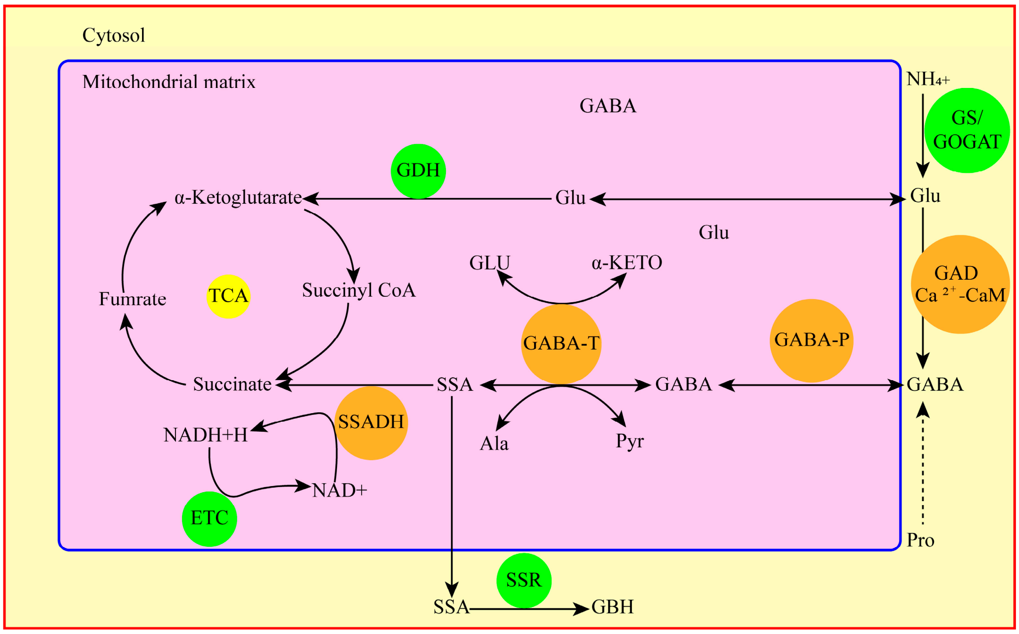

Figure 1. Biosynthesis of GABA in plants by GABA shunt. Figure modified from Ramos-Ruiz et al. [31].

3. GABA Transport in Plants

GABA transporters play vital roles in the accumulation and metabolism of GABA in cells. A family of membrane-bound transport proteins mediates GABA transport across cellular membranes. GABA transporters are divided into two main classes based on substrate specificity: high-affinity transporters (GATs) and low-affinity transporters (LATs) [32]. In *Arabidopsis thaliana*, GAT1 and GAT2 are high-affinity GABA transporters, whereas LAT1 is a low-affinity GABA transporter [33]. GABA transporters are expressed in various plant tissues, including roots, leaves, and flowers. Furthermore, GABA is synthesized in the cytosol, and its accumulation in the vacuole requires the activity of GABA transporters [14,33]. The subcellular localization of GABA transporters can affect the accumulation of GABA in different organelles. For instance, the high-affinity GABA transporter GAT1 is localized in the plasma membrane, and its activity is essential for GABA uptake in root cells under stress conditions [34]. On the other hand, the low-affinity GABA transporter LAT1 is localized in the tonoplast, responsible for GABA's sequestration into the vacuole [35].

4. Potential Role of GABA in Abiotic Stress Tolerance in Horticultural Plants

GABA has been studied under various abiotic stress conditions, including drought, salinity, extreme temperatures, and heavy metals. This study examined the effects of GABA and its response factors under different abiotic stress conditions. Based on the results of studies conducted across diverse horticultural crops, Figure 2 and Table 1 show the influence of GABA on abiotic stress responses.

4.1. Application of GABA to Alleviate the Effects of Heat Stress

Global warming has increased significantly in recent times and may lead to substantial economic losses in the future [36]. Heat stress has emerged worldwide as a significant constraint on crop growth and yield. It adversely affects plant growth, mineral nutrient content, and yield. Furthermore, plants may display various symptoms under heat stress, such as oxidative damage, ultrastructural alterations, chlorophyll degradation, and photoinhibition [37]. The regulatory function of GABA in heat tolerance in plants has been investigated in numerous studies. It has been observed that GABA induces alterations in the antioxidant defense system, metabolic homeostasis, and heat shock factor pathway, ultimately enhancing heat tolerance [38,39].

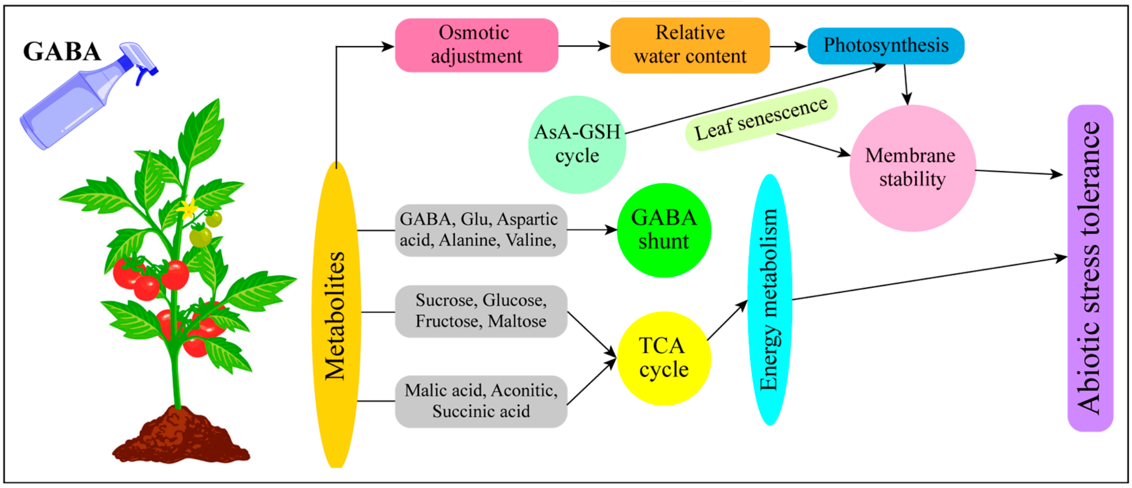

Figure 2. A diagrammatic representation reveals the potential of GABA supplementation in improving plant stress resilience.

Recent research on plants suggests that the external application of GABA can protect plant seedlings from heat stress by bolstering their antioxidant defense systems [40,41]. A study on creeping bentgrass foliage showed that GABA promoted heat tolerance by regulating osmotic potential, metabolic homeostasis, and the tricarboxylic acid cycle [40]. Furthermore, the application of GABA has been linked to the upregulation of *AER*, *ACS*, *CA1*, and *CAD3*, and GABA is involved in the biosynthesis of lignin and lipids, water usage, photosynthesis, and antioxidant defense potential. These genes have been found to improve HSF pathways and phenylpropanoid biosynthesis in perennial creeping bentgrass, thereby enhancing its heat tolerance [42]. GABA is a highly effective method for increasing the heat tolerance of creeping bentgrass by improving its heat tolerance with the application of GABA. In addition, this is achieved by improving photosynthesis and water balance and mitigating oxidative damage caused by high-temperature stress. Exogenous GABA has been observed to increase the transcript levels of genes that encode heat shock proteins, heat shock factor HSFs, and ascorbate peroxidase 3 under heat stress. Conversely, the inhibition of GABA biosynthesis has been found to suppress the expression of these genes [43]. Another study reported that foliar treatment with GABA efficiently relieved the harmful effects of heat stress in creeping bentgrass. A recent study has shown that GABA can also significantly enhance the expression of heat-induced *HSPs* and *HSFs*, as well as the abundance of *HSP101*, *HSP70*, and *HSP90-1* in the leaves of creeping bentgrass [44].

Recent studies have reported that GABA can enhance heat tolerance by inducing changes in proteomic profiles in creeping bentgrass. Likewise, GABA treatment has been linked to an increased accumulation of sugars and amino acids, such as PFK5, FK2, BFRUCT, RFS2, and ASN2. These changes in metabolism are critical for the energy supply and oxaloacetate pathways, which are involved in heat tolerance [45]. Another study indicated that the administration of GABA under heat stress enhanced the endogenous levels of GABA, glutamic acid, and threonine in creeping bentgrass. This mechanism governs the regulation of the GABA shunt and oxaloacetate pathway, resulting in improved heat tolerance [46]. Similarly, the exogenous treatment of GABA application has been found to significantly contribute to the accumulation of polyphenols, particularly catechins, upregulate genes related to flavonoid metabolism in tea seedlings under heat stress conditions, and improve the antioxidant system [38]. Recent research on GABA has shown that GABA enhances the adaptability of roots to heat stress by boosting their antioxidant capacity, vitality, and osmotic adjustment. In addition, GABA regulates metabolites under heat stress, enhancing antioxidant capacity, energy metabolism, cellular structures, and osmotic balance in the roots [47]. These findings imply that the exogenous administration of GABA can improve plant growth and survival in the face of heat stress by ameliorating antioxidant capacity and lowering oxidative damage.

4.2. Application of GABA to Alleviate the Effects of Cold Stress

Stress caused by low temperatures is a major impediment to plant growth and development, eliciting a cascade of physiological, biochemical, and molecular changes [48,49]. The consequences of cold stress are manifold and detrimental, including leaf wilting, chlorophyll loss, hampered photosynthesis, impaired cell membrane fluidity, reduced enzyme activity, metabolic disruption, and stunted growth [50]. Low temperatures also result in the production of highly active and toxic reactive oxygen species (ROS), such as hydrogen peroxide (H_2O_2), superoxide radicals (O^{2-}), and hydroxyl radicals (OH^-). The generation of ROS is attributed to membrane-bound electron transport and multiple metabolic pathways. As a result of these ROS, plant membrane fluidity is reduced, and macromolecules such as lipids, proteins, and nucleic acids are targeted, ultimately resulting in oxidative damage [51]. Consequently, maintaining the integrity and stability of the cell membrane structure is critical for a plant's adequate growth and development [52].

Numerous studies have reported the beneficial effects of GABA treatment in alleviating the adverse effects of cold stress on different crop species. Scientific evidence has shown that GABA can alleviate chilling injury in tomato seedlings by modulating antioxidant enzyme activity and scavenging reactive oxygen species (ROS) [53]. Furthermore, GABA has been found to enhance the low-temperature tolerance of tea plants and modulate various physio-biochemical processes under optimal conditions. These processes include the modulation of antioxidant activity, elevated SPAD values, chlorophyll fluorescence transients, and improved membrane stability [54]. Exogenous GABA treatment has also been beneficial during the postharvest storage of various fruits, including zucchini, banana, and peaches. It has been found that GABA can regulate weight loss, the chilling injury index, and cell death in zucchini fruits stored at 4 °C while simultaneously maintaining a lower rate of electrolyte leakage at these temperatures [55]. In addition, the pre-harvest application of spermine and GABA has been found to effectively prevent chilling damage and delay senescence in plants by increasing the proline content, boosting cellular antioxidant capacity, scavenging ROS, and improving cell membrane integrity and fluidity [56].

According to a study conducted by Li et al. [57], treatment with GABA has been shown to protect pear fruits against peel browning during extended storage periods at low temperatures. This was evidenced by lower browning indices, decreased levels of ROS and malondialdehyde, and increased antioxidant enzyme activity. Moreover, GABA application increases GABA shunt activity, promotes glycine betaine accumulation, and increases ATP production in cut flowers of *Anthurium* spp. [58]. In addition, Wang et al. [59] reported that GABA treatment ameliorated membrane damage, elevated antioxidant capacity, and reduced chilling injury in the banana peel. Furthermore, in peach fruit, GABA treatment was found to reduce chilling injury and the weight loss rate and maintain firmness and the total soluble solids content by suppressing the production of ROS and increasing the activity and gene expression of methionine sulfoxide reductase A (MSRA), thioredoxin reductase (TrxR), and methionine sulfoxide reductase B (MSRB). GABA application boosted the NADPH/NADP ratio, increased *G6PDH* and *6GPDH* gene expression, and increased G6PDH activity. This suggests that GABA induces the MSR-TrxR system, reducing chilling injury in peaches [60]. Together, these results indicate that GABA application can help to mitigate chilling injury in horticultural plants by regulating various physiological, biochemical, and molecular mechanisms.

4.3. Application of GABA to Alleviate the Effects of Salt Stress

Salinity has emerged as a major problem restricting the growth and development of various plants [61,62]. According to a report published by the FAO (2016), salt stress has caused damage to 45 million hectares of irrigated land worldwide or 19.5% of the total irrigated area. Salt stress negatively affects various morphological, physiological, and biochemical processes in plants, ultimately reducing their ability to absorb water, resulting in cell damage from the buildup of ions, stunting leaf growth, lowering photo assimilates available, and delaying germination [63,64]. Salt stress triggers an overproduction of reactive oxygen species (ROS), primarily in peroxisomes, chloroplasts, and mitochondria, which can result in lipid peroxidation and damage to biomolecules [65]. Additionally, Barbosa et al. [66] demonstrated that the administration of GABA during salt stress can modify the activities of antioxidant enzymes involved in N metabolic pathways and affect the signaling of the nitrate uptake system [67]. Studies confirm that GABA is a promising natural chemical critical in enhancing plant resilience to abiotic stresses, including plant salt stress tolerance.

The study conducted by Wu et al. [68] demonstrated that exogenous GABA application improves the tomato seedlings' capacity to withstand salt stress. This action is also strongly related to a decreased Na^+ transport from roots to leaves, an increased amino acid content, and the augmentation of antioxidant metabolism. In addition, when cucumber roots were exposed to salt stress, the administration of 5 mmol L^{-1} GABA dramatically reduced the accumulation of sodium ions. This suggests that applying exogenous GABA affects the absorption and inhibition of mineral elements in cucumber seedlings under NaCl stress. Previous studies have also found that GABA accumulation rapidly increases in tomato and tea plants when anabolic metabolism is activated by salt stress induction [69]. GABA reduces salt damage during white clover seed germination by increasing starch catabolism, utilizing sugar and amino acids for growth maintenance, increasing Na^+/K^+ transportation for osmotic adjustment, and enhancing antioxidant defense potential under salt stress [70]. Exogenous GABA inhibits H_2O_2 generation and reduces oxidative damage in salt-stressed *Caragana intermedia* roots by regulating the expression of key genes involved in H_2O_2 and peroxidase production [27].

Exogenous treatment with GABA has been shown to positively impact muskmelon seedlings under saline–alkaline stress by improving the structure and functions of Photosystem II [71]. Furthermore, GABA has been found to mitigate $Ca(NO_3)_2$-induced damage in muskmelon seedlings by enhancing $NO_3{}^-$-N absorption and assimilation while boosting endogenous GABA levels, suggesting its potential role as a temporary nitrogen repository in protecting plants from salt stress [72]. Exogenous GABA treatment at a concentration of 0.5 mM can also mitigate alkaline stress in apple seedlings by promoting growth and scavenging ROS activities, improving photosynthetic properties and total chlorophyll levels [73]. Furthermore, GABA has been found to enhance NO levels in muskmelon under salinity–alkalinity stress by boosting NR and NOS activities, which may help to regulate the Na^+/K^+ balance, enhance antioxidation, maintain the stability and integrity of cell membranes, and ultimately improve muskmelon tolerance to salinity–alkalinity stress [74]. Additionally, GABA application can effectively reduce the salt damage index and increase the resistance of plants to NaCl stress. The diverse expression of *MuGABA-T* in Arabidopsis and its overexpression in hairy mulberry roots decreased GABA levels in transgenic plants and increased their sensitivity to salt stress, indicating the importance of GABA in alleviating the negative effects of salt stress [75]. The exogenous application of GABA and GSH increases the salt tolerance of *C. annuum* by enhancing antioxidant defense systems, ATPase enzymes, and *CaXTH* stress-related genes [76]. Given the increasing threat of soil salinity to global food security, it is crucial to explore innovative approaches, such as GABA supplementation, to enhance the resilience of crops to saline conditions.

4.4. Application of GABA to Alleviate the Effects of Drought Stress

Drought stress is a critical environmental factor that impedes the growth and development of various crops, including fruits and vegetables [6,77,78]. Long-term drought causes a decline in the relative water content and various metabolic and photosynthetic abnormalities [79,80]. The protective effect of GABA against drought stress in plants is attributed to its ability to increase osmolytes and leaf turgor and regulate antioxidants to reduce oxidative damage. Increasing GABA production in guard cells reduces stomatal opening and transpiration, and regulating the release of tonoplast-localized anion transporters improves water use efficiency and drought tolerance [10,81]. The drought stress tolerance of various plant species, such as apples [82], tomatoes [83], and grapevines [84], can be improved by applying exogenous GABA, as demonstrated in previous studies. The optimal dosage and application method of GABA for achieving maximum drought stress tolerance may differ depending on the plant species and environmental conditions.

Upregulating the expression of genes related to the 'Biosynthesis of secondary metabolites', 'Carbon fixation in a photosynthetic organism', 'Glutathione metabolism', and 'MAPK signaling pathway' might be a mechanism by which GABA enhances plant drought resistance, as revealed by transcriptomics analysis. These findings indicate that applying exogenous GABA can enhance drought tolerance and improve apple fruit quality [13]. In addition, GABA application has been found to enhance the water use efficiency and nitrogen use efficiencies of various crops, including lettuce [85], strawberry [86], white clover [87], and black cumin [88]. Using the exogenous application of GABA into white clover plants improved drought tolerance by increasing the endogenous GABA content, polyamines, and proline metabolism through upregulating the GABA shunt, polyamines, and proline metabolism [89]. In addition to its effect on osmoregulation (e.g., soluble sugars and proline content), increased levels of GABA also contribute to an enhanced chlorophyll content and antioxidant enzyme activity in black cumin plants in response to water-deficit-induced stresses [88]. Overall, recent studies have suggested that GABA has significant potential as a target for improving drought stress tolerance in horticultural crops. However, further research is needed to optimize GABA application methods and dosages to maximize crop efficacy.

4.5. Application of GABA to Alleviate the Effects of Heavy Metal Stress

Heavy metal pollution is a frequent outcome of natural and human activities such as urbanization, rapid industrialization, and mining, leading to disruptions in eco-environmental sustainability and a decrease in global plant productivity [90]. In recent decades, soil contamination by heavy metals (Zn, Ni, Fe, Cr, Co, Pb, Cd, Hg, and As) resulting from agricultural activities has raised serious concerns regarding their potential threat to human health through direct intake and bioaccumulation in the food chain, as well as their impact on ecological systems [91]. In addition, the excessive accumulation of heavy metals in plant tissues can interfere with crop productivity by impairing several biochemical, physiological, and morphological functions [92]. GABA is a promising natural compound that is environmentally friendly and mass-producible, making it highly applicable in various areas [93]. Numerous studies have reported the potential of GABA in detoxifying heavy metals in plants [94–97]. For instance, exogenous GABA treatment in *Malus huphehensis* activates the GABA shunt, leading to a significant increase in the content of malate, citric acid, and sucrose, as well as the activity of several enzymes. This contributes to mitigating biomass decreases, root growth inhibition, and oxidative stress caused by alkaline stress [73]. Furthermore, exogenous GABA application effectively alleviates Cd toxicity in apple seedlings, lowering the Cd content and decreasing the expression of Cd uptake and transport-related genes [23]. These findings highlight the potential of GABA to mitigate the adverse effects of heavy metal pollution and promote plant growth in horticultural crops.

4.6. Some Other Stresses

Numerous studies have reported diverse effects of GABA supplementation on plants' physiological, biochemical, and molecular responses under various abiotic stresses (Table 1, Figure 3). Exogenous GABA modulates polyamine biosynthesis and degradation in melon roots under root-zone hypoxia stress [98]. GABA treatment in *Prunus* species enhances the photosynthetic rate, stomatal conductance, and total chlorophyll content, induces the transcriptional activities of *GAD2* and *GAD4* in roots, and affects leaf H_2O_2 levels and endogenous GABA, Glu, and alanine contents in a genotype- and organ-specific manner, thus mitigating the adverse effects of oxygen deficiency on roots [99]. In addition, GABA-induced salinity–alkalinity tolerance is associated with elevated H_2O_2 levels acting as a signal molecule, whereas AsA and GSH act as antioxidants to maintain membrane integrity, which is essential for ordered chlorophyll biosynthesis. In response to salinity–alkalinity stress, the excessive accumulation of chlorophyll and its precursors, a consequence of excessive chlorophyll oxidation, is mitigated by exogenous GABA pretreatment [26].

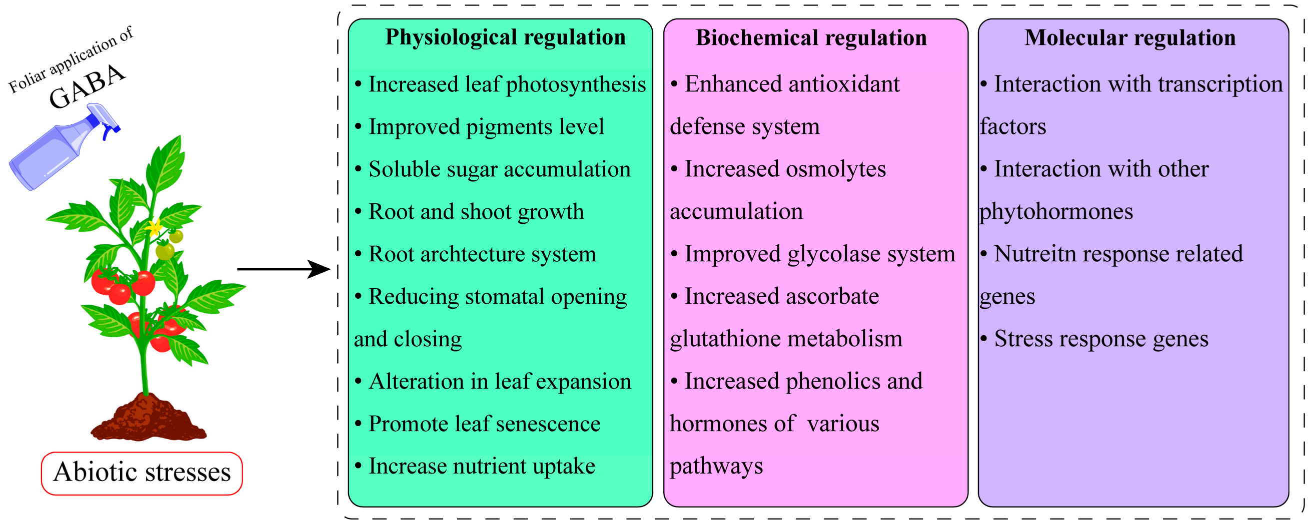

Figure 3. Effect of GABA supplementation on plants' physiological, biochemical, and molecular responses.

Table 1. GABA is a potential target for improving the abiotic stress tolerance of horticultural crops.

Crop	Stress	Reported Effect	References
Tomato and Brinjal	Heavy metal stress	The combination of GABA and nitric oxide (NO) can mitigate the toxicity of heavy metals and increase the stress tolerance in tomato and brinjal seedlings.	[100]
Apple	Drought stress	Improved apple quality under drought stress, modulation of endogenous GABA and polyamines.	[101]
Grapevine	Water stress	GABA accumulates at high levels in grapevine tendrils and promotes tendril coiling independently of jasmonates.	[84]
Piper	GABA	GABA priming reduced lipid peroxidation and improved the activity of antioxidant enzymes, photosynthesis, and mitochondrial function during osmotic stress.	[102]
Cucumber	Iron-deficient	GABA application in iron-deficient cucumber plants increased iron-uptake-related gene expression and auxin content via an auxin-dependent mechanism.	[103]
Lettuce	Salinity stress	Improved germination and plant growth, increased photosynthetic efficiency, enhanced activities of CAT, APX, and SOD enzymes, and controlled hydrogen peroxide levels under salinity stress.	[85]
Strawberry	Salinity stress	Improved the physiological and molecular response of strawberry plants to salinity stress by reducing ROS levels, increasing antioxidant enzyme activity, and upregulating the expression of stress-responsive genes.	[86]

Table 1. *Cont.*

Crop	Stress	Reported Effect	References
Citrus	Water stress	Exogenous GABA treatment of citrus plants led to increased endogenous GABA levels, enhanced respiration, and upregulation of phytohormone biosynthesis genes, indicating that GABA works harmoniously with phytohormones to reduce plant stress.	[19]
Creeping bentgrass	Heat stress	GABA can potentially enhance heat tolerance by regulating various physiological processes and metabolic pathways. These include boosting antioxidant metabolism, preventing leaf senescence, maintaining a balance between photosynthesis and transpiration, and improving osmotic adjustment. GABA also accumulates amino acids, carbohydrates, organic acids, and alcohol.	[40]
Creeping bentgrass	Heat stress	GABA's improved heat tolerance was linked to the biosynthesis of phenylpropanoids and the enhancement of HSF pathways. Additionally, the upregulation of genes such as *CAD3*, *ACS*, *AER*, and *CA1*, which are involved in lignin and lipid biosynthesis, photosynthesis, water use, and antioxidant defense, further contributed to this effect.	[42]
Creeping bentgrass	Heat stress	The exogenous application of GABA increased endogenous GABA content, effectively mitigating plant heat damage. The leaves displayed higher relative water content, improved photosynthesis, and cell membrane stability.	[43]
Creeping bentgrass	Heat stress	The application of GABA alleviated the damage and loss of chlorophyll caused by heat stress in creeping bentgrass by enhancing its antioxidant capacity.	[44]
Creeping bentgrass	Heat stress	The performance of creeping bentgrass under heat stress was improved by foliar application of GABA, proline, or N, which was found to regulate amino acid metabolism.	[46]
Tea	Heat stress	Under heat-stress conditions, GABA is instrumental in tea plants' polyphenol accumulation and antioxidant system upregulation.	[38]
Creeping bentgrass	Heat stress	GABA has effectively mitigated the reduction in overall antioxidant capacity caused by heat stress and enhanced various antioxidant enzyme functions, root vigor, and osmoregulation capabilities in root systems.	[47]
Tomato	Chilling stress	GABA administration safeguards tomato seedlings against cold stress by boosting the activity of specific antioxidant enzymes and lowering MDA levels, which helps to preserve membrane stability.	[53]
Tea	Cold stress	GABA successfully enhanced the resilience of tea plants to low temperatures and maintained the optimal functioning of numerous physiological and biochemical processes. Increased SPAD measurements, chlorophyll fluorescence dynamics, membrane stability, and the regulation of antioxidant activities evidence this.	[54]

Table 1. *Cont.*

Crop	Stress	Reported Effect	References
Gerbera cut flowers	Low temperature	Applying appropriate concentrations of GABA and SPER pre-harvest can enhance the quality and longevity of gerbera-cut flowers while reducing cold-related damage to a minimum using GABA treatment.	[56]
Pear	Low temperature	Fruit exposed to GABA experienced slower browning, reduced browning indices, and lower levels of reactive oxygen and malondialdehyde content. Additionally, GABA-treated fruit exhibited increased activity of peroxidase, superoxide dismutase, alternative oxidase, and catalase enzymes, as well as elevated gene expression related to these enzymes.	[57]
Anthurium cut flowers	Chilling stress	A reduction in H_2O_2 accumulation was observed in anthurium cut flowers subjected to GABA treatment. This was due to increased activity in antioxidant enzymes such as superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), and glutathione reductase (GR).	[58]
Banana	Chilling stress	GABA administration significantly contributes to mitigating cold-related damage in banana fruit by promoting proline accumulation and reinforcing the antioxidant defense system.	[59]
Peach	Chilling stress	GABA application helped to reduce the increase in chilling injury (CI) index and weight loss rate while also slowing the deterioration of firmness and total soluble solids content in peaches subjected to cold conditions.	[60]
White Clover	Salt stress	The priming of white clover seeds using the right concentration of GABA can effectively mitigate salt's adverse effects on seed germination.	[70]
Muskmelon	Salinity–alkalinity stress	GABA could be essential in safeguarding the structure and functionality of chloroplasts and Photosystem II (PSII) from the harmful impact of combined salt and alkaline stress.	[71]
Muskmelon	Salinity–alkalinity stress	GABA application safeguarded muskmelon seedlings against the effects of combined salt and alkaline stress by boosting the activity of antioxidant enzymes and decreasing malondialdehyde levels.	[72]
Apple	Alkaline stress	Compared to the untreated control, external GABA application notably enhanced biomass, root development, and reactive oxygen species neutralization activities in apple seedlings exposed to alkaline stress.	[73]
Mulberry	Salt stress	Applying GABA externally to transgenic plants led to a considerable increase in antioxidant enzyme activities and reduced active oxygen-related damage under conditions of NaCl stress.	[75]

Table 1. *Cont.*

Crop	Stress	Reported Effect	References
Apple	Drought stress	A total of 0.5 mM GABA proved to be most successful in alleviating drought stress. As a result, GABA decreased superoxide anions and hydrogen peroxide buildup in leaf tissues during drought conditions while increasing POD, SOD, and CAT activity and the amount of GABA in leaf tissues.	[82]
Black cumin	Drought stress	Administering GABA can enhance the growth and productivity of black cumin even when exposed to water deficit stress conditions.	[88]
White Clover	Drought stress	Boosting endogenous GABA levels through the external application of GABA may enhance white clover's drought tolerance by positively regulating the GABA-shunt pathway and polyamines (PAs) and proline (Pro) metabolism.	[89]
Apple	Cadmium stress	Administering external GABA led to a marked reduction in net Cd^{2+} fluxes within apple roots and effectively lowered Cd content in roots subjected to Cd stress.	[23]

5. Conclusions

The protective role of GABA in stress tolerance in horticultural plants has been extensively studied in recent years, and the findings have been promising. Studies have demonstrated that the exogenous application of GABA improves the tolerance of horticultural plants to various abiotic stress factors, such as drought, high salinity, and extreme temperatures. These findings suggest that GABA could be a valuable tool in improving crop yields and quality in horticultural plants. In conclusion, the research on GABA in horticultural plants has advanced significantly in recent years. However, further research is needed to fully understand the molecular mechanisms underlying the protective effects of GABA in stress tolerance and to develop practical applications for horticulture. This review article provides a comprehensive resource for researchers and practitioners in horticulture and crop improvement, highlighting the current state of knowledge and future directions for research in this area.

Author Contributions: J.L., M.A.S. and F.H., conceptualization; F.H., U.K., F.K. and N.A. contributed to writing and original draft preparation; S.I., Y.P., H.U.J., X.M., J.A. and M.A.A. edited the manuscript; J.L., P.T., M.A.S. and J.C. contributed to supervision, project administration, and funding acquisition. All authors have read and agreed to the published version of the manuscript.

Funding: We are grateful to the Guangdong Science and Technology Project (2018B020202009 and 2022B0202070002), Guangdong Provincial Special Fund for Modern Agriculture Industry Technology In-novation Teams (2023KJ108).

Data Availability Statement: Not applicable.

Acknowledgments: Thanks to all researchers for their contribution to this work.

Conflicts of Interest: The authors declare no conflict of interest.

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