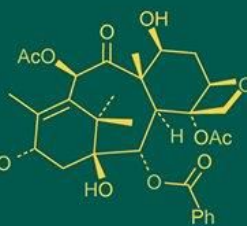


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Unraveling neurotransmitter mediated signaling in horticultural plants under abiotic stress conditions

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Abstract

Plants are consistently subjected to various abiotic stresses, including drought, salinity, temperature fluctuations, heavy metal exposure, and nutrient deficiencies, which considerably hinder their growth, productivity, and overall global food security. Beyond traditional phytohormones, mounting evidence emphasizes the crucial functions of evolutionarily conserved neurotransmitter-like substances such as melatonin, acetylcholine (ACh), dopamine, and γ -aminobutyric acid (GABA) in orchestrating plant responses to stress. These bioactive agents operate as versatile signaling molecules that harmonize redox balance, ion transport, metabolic control, and transcriptional adjustments in response to challenging environmental circumstances. Melatonin, initially discovered in the human pineal gland and subsequently in plants, serves as a powerful antioxidant while influencing mitogen-activated protein kinase (MAPK) pathways, hormonal interactions, and reactive oxygen species (ROS) signaling to bolster resilience against drought, salinity, chilling, heavy metals, and nutrient-related stress. Acetylcholine plays a role in regulating ion movement, membrane depolarization, and systemic signaling, thereby aiding in growth modulation and adaptive responses to stress. Dopamine, a catecholamine that originates from tyrosine, boosts antioxidant capabilities, preserves ion and hormonal equilibrium, and enhances photosynthetic efficiency in the face of drought, salinity, cold, and nutrient scarcity. In a similar vein, GABA, which is primarily produced through the GABA shunt pathway, connects carbon and nitrogen metabolism with stress signaling, facilitating osmotic adjustment, antioxidant protection, and metabolic stability. Together, these neurotransmitter-like compounds orchestrate physiological, biochemical, and molecular processes that strengthen plant resilience in horticultural crops. Gaining insights into their biosynthesis, signaling networks, and interactions with established hormonal and redox pathways opens new avenues for creating sustainable strategies aimed at improving crop performance in the face of evolving climatic conditions.

Keywords: Plant neurotransmitter, melatonin, acetylcholine, dopamine, GABA, biosynthesis, abiotic stress

1. Introduction

Plants face several environmental stresses, with abiotic factors posing a persistent and progressively intensifying threat to global food security. Owing to their sessile nature, plants are inherently vulnerable to adverse environmental fluctuations, resulting in yield reductions of 50-70%, particularly across Asia (Matthews *et al.*, 1997) [59]. Enhancing plant resilience traits to combat these abiotic stressors has become the need of the hour with critical scientific priority. Under field conditions, plants are frequently subjected to the multiple abiotic stresses, such as drought, heat, salinity, etc. which are often more detrimental to crop growth, development, and productivity than individual stresses alone (Fahad *et al.*, 2017) [21]. Extensive studies on plant-environment interactions have paved the way for targeted interventions designed to optimize the stress-tolerance potential of diverse crops (Gull *et al.*, 2019) [28]. One such promising strategy, the exogenous application of plant growth regulators, hormones, and other biostimulatory compounds, has gained increasing attention for enhancing abiotic stress tolerance (Ahammed *et al.*, 2020a) [107]. In this context, emerging evidence indicates that neurotransmitters constitute an evolutionarily conserved class of bioactive signaling molecules that modulates cellular homeostasis, signal transduction pathways, redox balance and stress-responsive pathways in plants (Roshchina, 2001) [71].

The widespread distribution of these molecules across biological kingdoms suggests that they function as conserved chemical messengers (Akula & Mukherjee, 2020) [3]. Acetylcholine, catecholamines (such as dopamine and norepinephrine), indoleamines (serotonin and melatonin), and compounds derived from amino acids (like glutamate and γ -aminobutyric acid, or GABA) represent major classes of plant neurotransmitters. It is recognized as multifunctional signaling molecules in plants, influencing a wide range of physiological and developmental processes. They regulate organ formation, flowering and reproductive events, membrane ion transport, photosynthetic efficiency, circadian rhythms, photomorphogenic responses, fruit maturation, and plant adaptation to changing environmental conditions (Roshchina, 2016) [72]. A comprehensive understanding of plant neurotransmitters' biosynthesis pathways, signaling mechanisms, and association with established hormonal and redox networks under abiotic stress is still lacking, despite mounting evidence for their regulatory roles. Addressing these gaps is essential for harnessing their potential in developing climate-resilient horticultural crops.

2. Melatonin

Melatonin (N-acetyl-5-methoxytryptamine) is a multifunctional indoleamine that present in both animals and plants. First isolated from the human pineal gland (Lerner *et al.*, 1958) [46], it was initially studied for its regulatory roles in animal physiology. In animals, melatonin is well known for orchestrating circadian and seasonal rhythms, such as those governing migration and reproduction. Subsequently, melatonin was independently detected in higher plants in two pioneering studies involving seeds and edible tissues (Hattori *et al.*, 1995) [30]. Since then, it has been identified across diverse plant taxa, ranging from algae and fungi to a broad spectrum of angiosperms, including both monocotyledonous and dicotyledonous species (Fernández-Alegre *et al.*, 2022) [22]. In plants, melatonin is now regarded as a putative phytohormone and a critical signaling molecule that regulates growth, development, and adaptive responses, particularly under biotic and abiotic stress conditions. Melatonin biosynthesis in plants has been localized primarily to chloroplasts (Zheng *et al.*, 2017) [105] and mitochondria (Wang *et al.*, 2017) [88], with additional evidence suggesting the possible involvement of cytosol. It is widely distributed among plant organs, with relatively higher concentrations reported in roots, flowers, fruits, seeds, and bulbs. Various horticultural and crop species, including cucumber, tomato, apple, banana, and onion, have been shown to accumulate detectable levels of melatonin (Nawaz *et al.*, 2016) [63]. Functionally, it acts as potent singlet oxygen scavenger (Schaefer & Hardeland, 2009) [75]. It readily traverses cellular membranes and localizes within subcellular compartments such as the nucleus and mitochondria (Tan *et al.*, 2016) [86]. Through direct radical scavenging and enhancement of cellular antioxidant systems, melatonin mitigates oxidative damage, restricts lipid peroxidation, stabilizes membrane integrity, and protects plant tissues against stress-induced injury, thereby functioning as an early protective molecule under adverse environmental conditions.

2.1 Biosynthetic pathway of melatonin

In plants melatonin biosynthesis originates from the amino acid tryptophan. In the primary pathway, tryptophan is first

decarboxylated by tryptophan decarboxylase (TDC) to produce tryptamine. Tryptamine is subsequently hydroxylated by tryptamine-5-hydroxylase (T5H) to form serotonin (5-hydroxytryptamine, 5-HT) (Kang *et al.*, 2007) [38]. From serotonin, melatonin synthesis proceeds through two alternative routes. In one pathway, serotonin is converted into N-acetylserotonin (NAS) by serotonin-N-acetyltransferase (SNAT), following a mechanism similar to that described in animals (Kang *et al.*, 2013) [37]. In another route, serotonin can be methylated to produce 5-methoxytryptamine (5-MT) via caffeic acid-O-methyltransferase (COMT) (Lee *et al.*, 2014) [45]. Interestingly, SNAT exhibits substrate flexibility. It can directly acetylate tryptamine to form NAS without serotonin as an intermediate and can also acetylate 5-MT to produce melatonin (Byeon *et al.*, 2013) [13]. The final step in melatonin biosynthesis involves the methylation of NAS to produce melatonin. This reaction is catalyzed either by N-acetylserotonin methyltransferase (ASMT) (Park *et al.*, 2013) [65] or by HIOMT (hydroxyindole-O-methyltransferase) (Byeon *et al.*, 2014) [108].

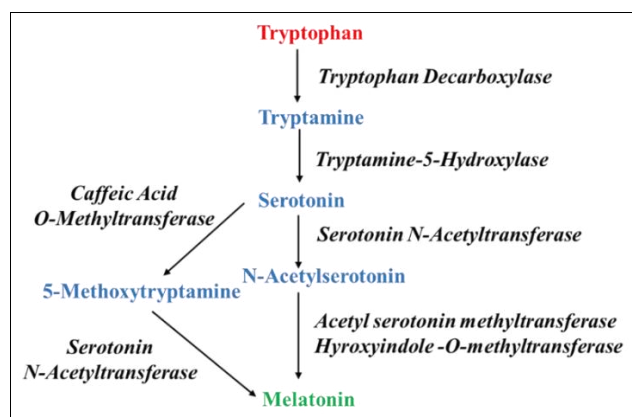


Fig 1: Biosynthetic route of melatonin

Melatonin in abiotic stress response

Building on its strong antioxidant capacity and specific subcellular localization, melatonin plays a pivotal role in regulating plant stress physiology. It enhances photosynthetic efficiency, protects the photosynthetic apparatus from excessive light exposure, preserves chloroplast integrity, and maintains cellular redox homeostasis. Beyond its direct antioxidative function, melatonin also modulates transcriptional regulation by influencing stress-responsive genes and epigenetically associated pathways (Mathur and Pramanik, 2020) [58]. Exogenous application of melatonin has been widely reported to enhance plant tolerance to multiple abiotic stresses, including salinity, drought, low temperature, heavy metal toxicity, and certain biotic challenges. These protective effects are mediated through coordinated interactions with phytohormones, signaling molecules, and transcription factors that collectively regulate adaptive stress responses. In addition to its regulatory functions, melatonin undergoes dynamic metabolism in plants through both enzymatic and non-enzymatic pathways (Zeng *et al.*, 2022) [101]. The precise signaling mechanisms of melatonin-derived metabolites in plants remain largely unresolved. It plays a significant role in mitigating drought-induced oxidative stress by enhancing photosynthetic efficiency, maintaining hormonal balance, regulating stress-responsive gene

expression, and promoting physiological adjustments. It strengthens antioxidant defense systems, sustains cellular water status, and ultimately contributes to improved stress tolerance and yield stability. Similarly, in Hibiscus, melatonin increases chlorophyll content and photosynthetic performance, partly through interaction with salicylic acid signaling (Yan *et al.*, 2023) ^[95], while in coffee plants it reduces chlorophyll degradation and electrolyte leakage under stress conditions (Cherono *et al.*, 2021) ^[15]. In *Salvia* species, melatonin not only alleviates stress injury but also enhances essential oil yield and composition (Bidabadi *et al.*, 2020) ^[10]. Foliar application of melatonin in *Moringa oleifera* improves yield and amino acid composition, thereby reducing the detrimental effects of drought stress (Sadak *et al.*, 2020) ^[73].

Beyond drought stress, melatonin also confers tolerance to salinity stress through multiple physiological and molecular mechanisms. Exogenous treatment increases fresh and dry biomass, limits chlorophyll degradation, maintains lower cellular sodium accumulation, and enhances antioxidant enzyme activity under saline conditions. It further induces the expression of salt stress-responsive genes, including the vacuolar Na⁺/H⁺ antiporter NHX1 and the potassium transporter AKT1. In tomato, melatonin application alleviates combined salinity and heat stress by reducing ROS accumulation, improving photosynthesis, maintaining stomatal function, and enhancing overall plant growth (Martinez *et al.*, 2018; Khan *et al.*, 2024) ^[57, 40]. Similar protective effects have been reported in *Ranunculus repens*, where 200 µM melatonin improved growth attributes,

enhanced peroxidase activity, reduced ROS levels, and delayed flower bud emergence under salinity stress (Eisa *et al.*, 2023) ^[19]. In tomato cultivars ‘Roma’ and ‘FM9’, melatonin mitigated salt toxicity by improving antioxidant capacity, growth parameters, and ion homeostasis (Ali *et al.*, 2021) ^[5]. Likewise, melatonin priming in potato alleviated salt-induced damage by enhancing stolon formation, maintaining tissue water content, regulating ion balance, and increasing the accumulation of proline, flavonoids, and carotenoids (Efimova *et al.*, 2023) ^[18]. Furthermore, melatonin treatment improves seed germination under saline-alkaline conditions by stimulating antioxidant enzyme activities, promoting osmolyte accumulation, and reducing oxidative stress (Wang *et al.*, 2023) ^[89]. Melatonin was found to alleviate chlorosis, decrease chlorophyll degradation, and stabilize photosynthetic rate by scavenging reactive oxygen species (ROS) and protecting chloroplasts in apple plants (Zheng *et al.*, 2021) ^[104]. In tomato, melatonin treatment in plants affected cell wall polysaccharide biosynthesis, glutathione metabolism, and redox homeostasis, leading to increased retention of chromium in the cell wall, improved chelation and sequestration of chromium, and enhanced antioxidant capacity to mitigate oxidative stress (Yang *et al.*, 2023) ^[96]. Overall, these findings establish melatonin as a key regulator of plant stress adaptation, coordinating metabolic stability, cellular protection, and growth maintenance under adverse conditions. A summary of the studied plant species, stress types, and corresponding physiological roles of melatonin is presented in Table 1.

Table 1: Role of exogenous melatonin in horticultural plants under abiotic stress tolerance

Plant species	Abiotic stress	Physiological role of melatonin	References
<i>Catharanthus roseus</i>	Heavy metal (Cadmium)	Improves seed germination, germination rate, seedling length, and vigour index	Nabaei <i>et al.</i> , 2019 ^[62]
<i>Brassica juncea</i>	Oxidative	Protects reproductive tissues	Tan <i>et al.</i> , 2007b
<i>Brassica oleracea</i>	Heavy metal (Copper)	Improves seedling growth and reduces lipid peroxidation	Posmyk <i>et al.</i> , 2008 ^[67]
<i>Cucumis sativus</i>	Temperature	Antioxidant scavenger & Maintain cellular integrity	Posmyk <i>et al.</i> , 2009 ^[66] , Xu <i>et al.</i> , 2010 ^[94]
<i>Solanum lycopersicum</i>	Salinity	Regulates photosynthetic machinery	Zhao <i>et al.</i> , 2016
<i>Solanum lycopersicum</i>	Thermotolerance	Enhance cellular protein protection	Xu <i>et al.</i> , 2016 ^[93]
<i>Solanum lycopersicum</i>	Drought	Promotes cuticle formation	Ding <i>et al.</i> , 2018 ^[17]
<i>Capsicum annuum</i>	Salinity	Increases the active of iron, Potassium, endogenous Nitic oxide and Hydrogen sulphide	Kaya <i>et al.</i> , 2020 ^[29]
<i>Malus hupehensis</i>	Alkalinity	Regulates polyamine synthesis	Gong <i>et al.</i> , 2017 ^[27]
<i>Prunus persica</i>		Drought tolerance, reduced chilling injury, post-harvest improvement	Gao <i>et al.</i> , 2016 ^[23]
<i>Actinidia deliciosa</i>	Thermotolerance	Promotes antioxidant enzyme and glutathione s-transferase transcription	Liang <i>et al.</i> , 2018 ^[49]
<i>Limonium bicolor</i>	Salinity	Improved seed germination	Li <i>et al.</i> , 2019 ^[47]

3. Acetylcholine

Acetylcholine (ACh) is an evolutionarily conserved bioactive molecule detected across diverse life forms, including bacteria, algae, fungi, mosses, and higher plants, indicating its early phylogenetic origin and fundamental biological significance. Although traditionally associated with neurotransmission in animals, accumulating evidence demonstrates that ACh and its metabolic enzymes are widely distributed throughout the plant kingdom. Early studies in *Urtica dioica* suggested a role for ACh in regulating water relations and photosynthetic processes. Subsequent biochemical investigations confirmed the

presence of ACh in multiple plant species and tissues, including mungbean roots, maize, pea, spinach, sunflower, and blue-green algae. Quantitative analyses further revealed that ACh levels are higher in actively growing tissues, supporting its involvement in developmental regulation. ACh as a non-neuronal signaling molecule of functional relevance in plants.

3.1 Biosynthesis and metabolic reprogramming

In plants, ACh is synthesized from choline and acetyl-coenzyme A (acetyl-CoA) through a single-step enzymatic reaction catalyzed by choline acetyltransferase (ChAT),

particularly active in young and metabolically dynamic tissues. Its cellular concentration is tightly controlled by acetylcholinesterase (AChE), which hydrolyzes ACh into choline and acetate (Sarangle *et al.*, 2024) [74]. Environmental factors modulate ACh biosynthesis. Light quality, in particular, plays a regulatory role, as red light enhances precursor incorporation into ACh compared with far-red light, suggesting phytochrome-mediated control.

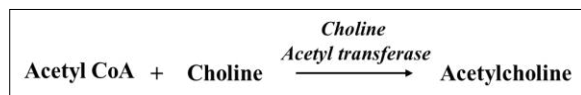


Fig 2: Simplified biosynthetic pathway of ACh

3.2 ACh signaling and Stress physiological functions

Emerging findings indicate that ACh plays a role in the signaling networks of plants. Pharmacological investigations utilizing muscarinic and nicotinic agonists and antagonists suggest the existence of receptor-like systems that exhibit characteristics akin to muscarinic (mAChR) and nicotinic (nAChR) receptors (Tretyn *et al.*, 1992) [109]. Computational studies have also identified potential nAChR homologs in tomato (*Solanum lycopersicum*) (Bamel and Mondal, 2023) [9], bolstering the notion of receptor-mediated cholinergic signaling within plants. ACh influences membrane permeability and ion fluxes involving H^+ , K^+ , Na^+ , Ca^{2+} , and Cl^- , thus affecting membrane depolarization, intracellular Ca^{2+} dynamics, and long-distance electrical signaling (Palee *et al.*, 2016) [64]. These ion-mediated mechanisms are crucial for the initiation of plant action potentials and systemic signaling (Sukhov *et al.*, 2011) [84]. Beyond its roles in electrophysiology, ACh has been associated with communication from roots to shoots (Brenner *et al.*, 2006) [12], the induction of rooting (Bamel *et al.*, 2007) [8], the progression of seedling development, the regulation of stomata, and the translocation of carbohydrates (Sugiyama *et al.*, 2011) [82]. Most studies on acetylcholine in plants have been conducted in agricultural and fodder crops, whereas investigations in horticultural crops remain limited.

4. Dopamine

Dopamine is a catecholamine present in both animals and plants. In humans, it plays essential roles in reward signaling, motor control, and hormonal regulation, and its dysregulation is associated with neurological disorders such as Parkinson's disease, schizophrenia, and depression. In plants, dopamine has emerged as an important growth-promoting and stress-mitigating molecule. Increasing evidence indicates that dopamine enhances plant tolerance to abiotic stresses including drought, salinity, nutrient imbalance, chilling, and oxidative stress (Allen, 2003; Liu *et al.*, 2020) [6, 54]. Dopamine possesses strong antioxidant properties and participates in multiple physiological processes through interactions with plant hormones and signaling networks. Its levels fluctuate during plant development and typically increase under stress conditions (Liang *et al.*, 2017; Zhang *et al.*, 2022) [50, 102-103].

4.1 Biosynthesis of dopamine

Dopamine ($C_8H_{11}NO_2$; molecular weight 153.18) is a nitrogen-containing, light-sensitive compound that readily oxidizes in the presence of oxygen (Howe & Dombeck, 2016) [31]. In plants, catecholamine biosynthesis resembles that of mammals and originates from the amino acid tyrosine (Kulma & Szopa, 2007) [42]. However, enzymatic

routes and regulation may vary among species. In plants, dopamine is synthesized in the cytoplasm from the amino acid tyrosine via two principal pathways.

In the decarboxylation pathway, tyrosine is first decarboxylated by tyrosine decarboxylase (TYDC) to form tyramine, which is subsequently hydroxylated by monophenol hydroxylase (MH) to produce dopamine. In the hydroxylation pathway, tyrosine is initially hydroxylated by tyrosine hydroxylase (TH) to generate L-DOPA, followed by decarboxylation by DOPA decarboxylase (DD) to form dopamine (Facchini & De Luca, 1995) [20]. Dopamine may further be converted into norepinephrine and epinephrine via dopamine β -hydroxylase-like and phenylethanolamine N-methyltransferase-like enzymes. Environmental factors significantly influence dopamine biosynthesis (Liang *et al.*, 2017) [50].

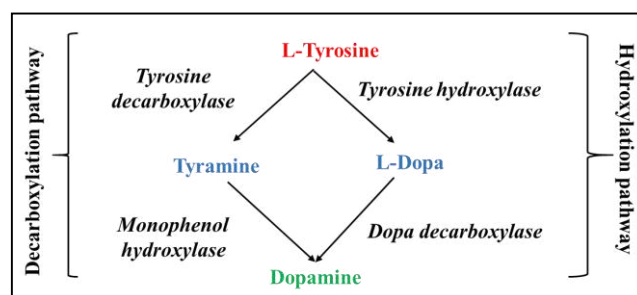


Fig 3: Dopamine biosynthetic pathway in plants

4.2 Dopamine in abiotic stress response

Overexpression of MdTyDC in apple increased endogenous dopamine levels and improved drought and salinity tolerance by enhancing antioxidant capacity, maintaining ion homeostasis, increasing ABA accumulation, and regulating transcription factors such as WRKY, ERF, and NAC (Gao *et al.*, 2021; Wang *et al.*, 2021; Liu *et al.*, 2023) [25, 91, 53]. These findings confirm that dopamine biosynthesis is tightly regulated at enzymatic and transcriptional levels. Drought stress disrupts photosynthesis, induces stomatal closure, impairs nutrient transport, and triggers excessive accumulation of reactive oxygen species (ROS). Exogenous dopamine application mitigates these effects by preserving chlorophyll content, enhancing photosynthetic rate, reducing H_2O_2 accumulation, and improving nutrient uptake and transport. In *Malus domestica*, dopamine treatment alleviated drought-induced growth inhibition by improving antioxidant enzyme activity, delaying leaf senescence, suppressing chlorophyll degradation genes (PAO, SAG12), and regulating transcription factors such as WRKY, ERF, and NAC (Liang *et al.*, 2018; Gao *et al.*, 2020) [49, 51, 24]. Dopamine also enhanced water-use efficiency (WUE), increased sucrose and organic acid accumulation, and modulated Ca^{2+} signaling pathways. Similarly, in *Solanum lycopersicum*, dopamine improved drought tolerance by upregulating antioxidant enzymes (SOD and CAT), reducing ethylene production, maintaining membrane integrity, and enhancing root biomass (Akçay *et al.*, 2024) [2]. Salinity stress disturbs ion balance and induces osmotic and oxidative damage. Dopamine regulates ion homeostasis by enhancing K^+/Na^+ and Ca^{2+}/Na^+ ratios and upregulating salt overly sensitive (SOS) pathway genes. It also promoted uptake of essential nutrients (N, P, K, S, Cu, Mn) and suppressed toxic ion accumulation. In tomato, dopamine increased indole-3-acetic acid (IAA) levels, reduced ABA

accumulation, regulated sugar metabolism, and improved salinity tolerance (Yildirim *et al.*, 2024) ^[97]. Chilling temperatures impair membrane stability and photosynthesis. In *Citrullus lanatus*, dopamine application enhanced chlorophyll content, proline accumulation, antioxidant enzyme activity, and polyamine metabolism, collectively improving chilling tolerance (Jiao *et al.*, 2021) ^[33]. In banana (*Musa sapientum*), dopamine treatment increased endogenous dopamine levels, suppressed chlorophyll degradation genes (MDC, PPH, PaO, RCCR), and enhanced

antioxidant enzyme activity, thereby reducing oxidative damage during chilling (Ali *et al.*, 2023) ^[4]. Table 2 presents a compilation of the documented horticultural species, their corresponding abiotic stress factors, and the physiological mechanisms modulated by dopamine. Overall, dopamine functions as a multifunctional growth regulator and stress-mitigating molecule in horticultural plants. These findings highlight its potential application as a sustainable biostimulant to improve horticultural crop productivity under changing climatic conditions.

Table 2: Role of exogenous dopamine in horticultural plants under abiotic stress tolerance

Plant species	Type of abiotic stress	Physiological role of dopamine	References
<i>Malus domestica</i> Borkh.	Drought	Greater photosynthesis and stress signalling	Gao <i>et al.</i> 2020b
<i>Malus domestica</i>	Drought	Elevated growth; lowered oxidative damage	Wang <i>et al.</i> 2021b ^[91]
<i>Solanum lycopersicum</i>	Drought	Antioxidant scavenger, root architecture	Akcay <i>et al.</i> , 2024 ^[2]
<i>Malus hupehensis</i>	Salinity	Stronger growth and salt resilience	Li <i>et al.</i> 2015 ^[110]
<i>Solanum lycopersicum</i>	Salinity	Regulate phytohormone signals (Auxin and ABA)	Yildirim <i>et al.</i> , 2024 ^[97]
<i>Malus domestica</i>	Salinity	Better root performance and salt resistance	Gao <i>et al.</i> 2020a
<i>Citrullus lanatus</i>	Cold	Polyamine metabolism	Jiao <i>et al.</i> 2020
<i>Musa sapientum</i>	Cold	Modulating chlorophyll degradation genes & ROS	Ali <i>et al.</i> , 2023 ^[4]

5. GABA

γ -Aminobutyric acid (GABA) is a four-carbon, non-proteinogenic amino acid widely distributed in autotrophic and heterotrophic organisms. It was first identified in potato tubers (Den *et al.*, 1947) and has subsequently been detected in plants, animals, fungi, and bacteria. GABA serves as a dual role as a metabolite and/or as a signalling molecule in plant growth, development, and stress responses (Bouche and Fromm 2004; Roberts, 2007) ^[11, 70]. GABA is rapidly and substantially accumulated in plants in response to both biotic and abiotic stress conditions (Scholz *et al.*, 2015) ^[76]. GABA acts as a priming agent by triggering diverse defense-associated signaling pathways in response to adverse environmental cues (Kinnersley and Turano, 2000) ^[41].

5.1 Biosynthesis of GABA

Chemically, GABA (C₄H₉NO₂; 103 Da) is synthesized primarily through the decarboxylation of L-glutamate via the GABA shunt pathway, catalyzed by glutamate decarboxylase (GAD) (Xu and Hu *et al.*, 2014) ^[92]. In

addition to this major pathway, GABA can also be produced from polyamines such as putrescine and spermidine through the action of diamine oxidase and polyamine oxidase [Shelp *et al.*, 2012] ^[78]. Within mitochondria, GABA is converted into succinic semialdehyde by GABA transaminase (GABA-T), which is subsequently oxidized to succinate by succinic semialdehyde dehydrogenase (SSADH). Succinate then enters the tricarboxylic acid (TCA) cycle, thereby linking the GABA shunt to central carbon metabolism. The mitochondrial membrane transporter GABA permease (GABA-P) facilitates the transport of cytosolic GABA into mitochondria, integrating the GABA shunt with the TCA cycle to provide energy and carbon skeletons (Michaeli *et al.*, 2011) ^[60]. The key enzymes of the GABA shunt such as glutamate GAD, GABA-T, and SSADH play crucial roles in maintaining ion homeostasis (Su *et al.*, 2019) ^[81], enhancing abiotic stress tolerance (Jalil *et al.*, 2017; Sita and Kumar, 2020) ^[32, 79], and regulating plant growth, development, and senescence.

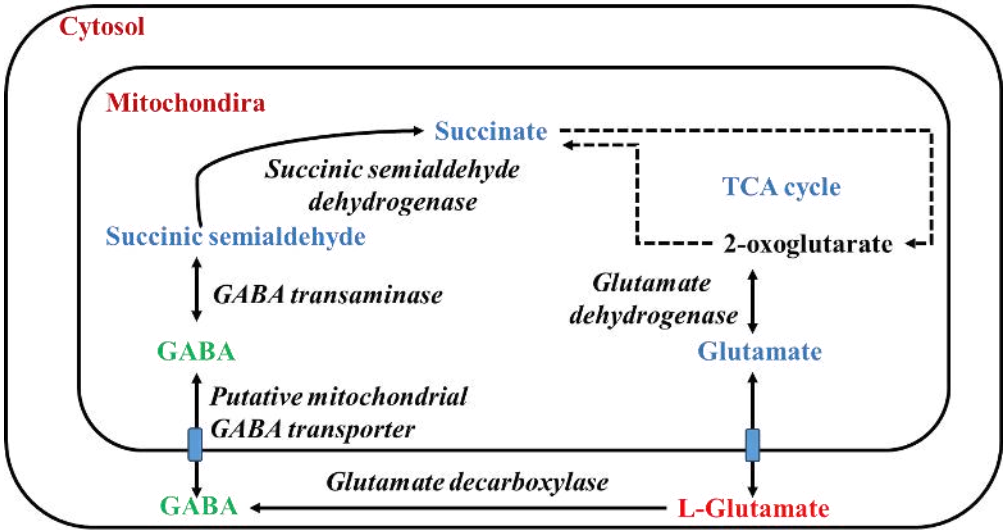


Fig 4: GABA biosynthetic pathway in plants

5.2 GABA response under abiotic stress

GAD is a Ca²⁺/calmodulin-binding protein whose activity is stimulated by elevated cytosolic Ca²⁺ levels and neutral pH in intact plants (Snedden *et al.*, 1995) ^[80]. GABA receptor genes in plants encode structural domains homologous to those found in animals (Lacombe *et al.*, 2001) ^[44]. Under stress conditions, GABA improves morphological and physiological traits, including enhanced photosynthetic efficiency and increased accumulation of osmoprotectants such as proline (Ma *et al.*, 2019) ^[55]. It also regulates

polyamine metabolism (Seifikalhor *et al.*, 2020) ^[77] and mitigates oxidative damage by activating antioxidant defense systems and modulating antioxidant enzyme gene expression (Kumar *et al.*, 2019) ^[43]. Under salt stress, GABA functions as a non-toxic osmolyte, reduces ROS accumulation, modulates the ascorbate-glutathione cycle, and improves saline-alkali stress tolerance (Jin *et al.*, 2019) ^[35]. In addition to drought, GABA has been reported to alleviate salinity, heat stress, chilling, low-temperature, and heavy metal stress, as summarised in Table 3.

Table 3: Role of exogenous GABA in horticultural plants under abiotic stress tolerance

Plant species	Abiotic stress	Physiological role of GABA	References
<i>Malus domestica</i>	Drought	Enhances water status, antioxidant enzymes, reduces ROS	Liu <i>et al.</i> , 2021 ^[52]
<i>Nigella sativa</i>	Drought	Improves growth under water deficit	Rezaei-Chiyaneh <i>et al.</i> , 2018 ^[69]
<i>Trifolium repens</i>	Drought	Regulates GABA-shunt, polyamines, proline metabolism	Yong <i>et al.</i> , 2017 ^[99]
<i>Lactuca sativa</i>	Salinity	Promotes germination, photosynthesis, antioxidant activity	Kalhor <i>et al.</i> , 2018 ^[36]
<i>Fragaria × ananassa</i>	Salinity	Limits ROS; induces stress-responsive genes	Golnari <i>et al.</i> , 2021 ^[26]
<i>Trifolium repens</i>	Salinity	Enhances seed germination under salinity	Cheng <i>et al.</i> 2018 ^[14]
<i>Morus alba</i>	Salinity	Reduces oxidative damage via enzyme activation	Zhang <i>et al.</i> , 2022 ^[102-103]
<i>Cucumis melo</i>	Alkalinity	Protects chloroplasts; strengthens antioxidant system	Chen <i>et al.</i> , 2018 ^[14]
<i>Agrostis stolonifera</i>	Heat	Maintains photosynthesis, osmotic balance, antioxidant capacity	Zeng <i>et al.</i> , 2021 ^[100]
<i>Camellia sinensis</i>	Heat	Stimulates polyphenols; supports antioxidant metabolism	Ren <i>et al.</i> , 2021 ^[68]
<i>Solanum lycopersicum</i>	Chilling	Stabilizes membranes; enhances antioxidant defense	Malekzadeh <i>et al.</i> , 2014 ^[56]
<i>Camellia sinensis</i>	Cold	Preserves physiological and biochemical stability	Zhu <i>et al.</i> , 2019 ^[106]
<i>Musa acuminata</i>	Chilling	Promotes proline; reduces oxidative injury	Wang <i>et al.</i> , 2014 ^[90]
<i>Prunus persica</i>	Chilling	Minimizes chilling injury; maintains fruit quality	Jiao <i>et al.</i> , 2022 ^[334]
<i>Pyrus communis</i>	Chilling	Delays browning; activates defense enzymes	Li <i>et al.</i> , 2019 ^[47]
<i>Anthurium andraeanum</i>	Chilling	Lowers H ₂ O ₂ via enzymatic regulation	Soleimani Aghdam <i>et al.</i> , 2016 ^[1]
<i>Gerbera jamesonii</i>	Chilling	Extends vase life; reduces cold damage	Mohammadi <i>et al.</i> , 2021 ^[61]
<i>Solanum lycopersicum</i>	Heavy metal	Decreases metal toxicity (with NO)	Suhel <i>et al.</i> , 2023 ^[83]

6. Future perspectives

Future studies should aim to clarify the exact perception and signaling pathways of melatonin, acetylcholine, dopamine, and GABA in plants, with a specific focus on identifying distinct receptors, transport systems, and downstream regulatory networks. A heightened focus on understanding their interactions with classical phytohormones and redox pathways is necessary to elucidate how these molecules fit into larger stress-response frameworks. Innovations in omics technologies, gene-editing techniques, and metabolic engineering present valuable opportunities to modify key biosynthetic genes and boost endogenous levels for enhanced stress resilience. Furthermore, extensive field trials and the creation of stable, economical formulations are crucial for converting laboratory insights into practical horticultural uses. In summary, the integration of neurotransmitter-focused strategies with breeding and sustainable crop management methods could greatly aid in the establishment of climate-resilient horticultural systems.

7. Conclusions

Neurotransmitter-like molecules, once thought to be exclusive to animal systems, are now acknowledged as essential components in the physiology of plant stress. Melatonin, acetylcholine, dopamine, and GABA serve as multifunctional regulators that harmonize antioxidant defense, ion balance, hormonal signaling, photosynthetic efficiency, and gene expression when plants face abiotic stress. Their biosynthetic pathways are finely tuned and responsive to environmental stimuli, allowing for a dynamic response to changing stress conditions. Experimental findings across various horticultural species indicate that the external application or internal enhancement of these

molecules significantly alleviates drought, salinity, temperature stress, heavy metal toxicity, and nutrient imbalances. By influencing ROS scavenging systems, MAPK signaling pathways, transcription factors, osmolyte accumulation, and metabolic processes, these compounds play a crucial role in enhancing growth, ensuring yield stability, and boosting stress resilience. Despite notable advancements, there are still gaps in our understanding of receptor-mediated perception mechanisms, downstream signaling elements, and the long-term effectiveness in field conditions.

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