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REVIEW

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Functions of dopamine in plants: a review

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ABSTRACT

Dopamine (3-hydroxytyramine or 3,4-dihydroxyphenethylamine) has many functions in animals, but also shows several other functions in plants. Since the discovery of dopamine in plants in 1968, many studies have provided insight into physiological and biochemical functions, and stress responses of this molecule. In this review, we describe the biosynthesis of dopamine, as well as its role in plant growth and development. In addition, endogenous or exogenously applied dopamine improved the tolerance against several abiotic stresses, such as drought, salt, and nutrient stress. There are also several studies that dopamine contributes to the plant immune response against plant disease. Dopamine affects the expression of many abiotic stresses related genes, which highlights its role as a multi-regulatory molecule and can coordinate many aspects of plant development. Our review emphasized the effects of dopamine against environmental stresses along with future research directions, which will help improve the yield of eco-friendly crops and ensure food security.

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3,4- dihydroxy phenethylamine; plant; biosynthetic pathway; abiotic stress; biotic stress

1. Introduction

Dopamine, along with norepinephrine and epinephrine, is a type of catecholamine found throughout the plant and animal kingdoms. Catecholamines are characterized as biogenic amines possessing a 3,4-dihydroxy-substituted phenyl ring, and are widespread in animals where they are well-known neurotransmitters.[1] Dopamine is a nitrogen-containing organic compound with the molecular formula of $C_8H_{11}NO_2$, its molecular weight is 153.18 (Figure 1a). It is sensitive to light and easy to oxidize in the presence of oxygen. In humans, dopamine serves a wide range of well-defined functions, including processes involved in reward, addiction, control of coordinated movement, metabolism, and hormonal secretion.[2] Correspondingly, the dysregulation of the dopaminergic system has been implicated in diseases such as schizophrenia; Parkinson's disease; depression; attention deficit hyperactive disorder; nausea and vomiting; and more recently, the autism spectrum disorder.[3,4]

Due to population growth and climate change, the negative effects of environmental stress on plant production increased in many regions of the world.[5] The abiotic stresses such as drought, salinity, and nutrient deficiencies severely affect the growth, development, and metabolism of plants.[6,7] Recently, many approaches have been used to overcome abiotic stresses in plants.[8] Chemical priming is a promising field in crop stress physiology. The use of compounds as initiators has been found to significantly improve plant tolerance to a variety of biological and abiotic stresses.[9]

Dopamine can promote the growth of plants under various stressful environments.[10–14] More recent studies have shown that dopamine can enhance tolerance to drought, salt stress, and nutrient deficiency in plants.[11–13] In addition, dopamine can improve the ability of plants to resist biological stressors. However, the number of articles on dopamine in plants is still small. The number of papers was less than 10 each year (Figure 1b). In order to better promote the development of this field, this paper reviewed the effects of dopamine on abiotic stress in plants, and provided the future research direction for the utilization of dopamine for sustainable production of crops.

2. Endogenous dopamine present in different plants

Considering the multiple function of dopamine in animals, investigation was carried out on the plants, and dopamine was detected in 1968.[1,15] Dopamine content varies considerably among species, from a few nanograms to several micrograms per gram. For example, dopamine is found at high concentration in the pulp of yellow banana (*Musa acuminata*), red banana (*Musa sapientum* var. *baracoa*), the spathes of *Araceae inflorescences*, fuerte avocado (*Persea americana*), and plantain (*Plantago major*).[1] However, the dopamine content in oranges, tomatoes, apples and other plants being relatively low, with a fresh weight of less than 1 μg per gram.[16,17] These notable variations of endogenous dopamine content among different plant species suggested that dopamine function varied from plant to plant. The content of dopamine in the number of plants is presented in Table 1.

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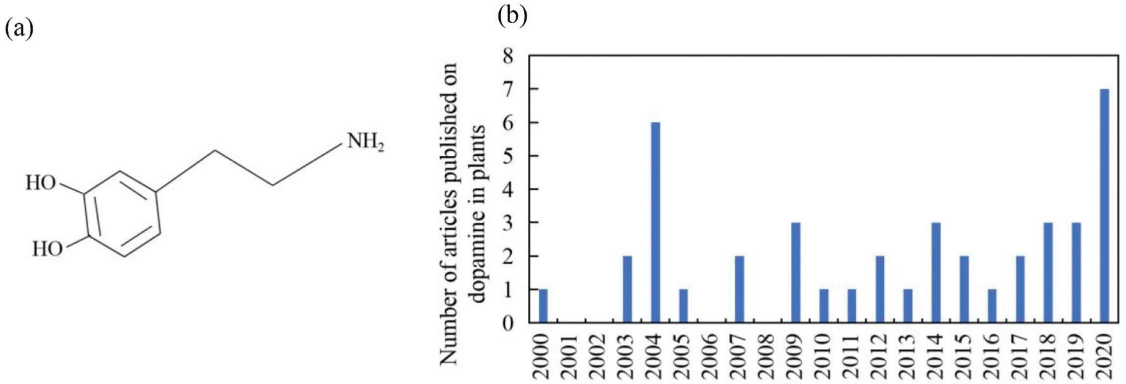

Figure 1. (a) Structures of dopamine and (b) evolution of the number of articles related with dopamine in plants from 2000 to 2020 (Jan to Sep).

Table 1. Dopamine content in different parts of plants.

Species	Detected Plant Parts	Dopamine content
Yellow banana (*Musa acuminata*)	Fruit pulp	42 µg/g FW
Red banana (*Musa sapientum* var. *baracoa*)	Fruit pulp	55 µg/g FW
Plantain (*Plantago major*)	Fruit pulp	5.5 µg/g FW
Fuerte avocado (*Persea americana*)	Fruit pulp	4 µg/g FW
Cavendish banana	Fruit pulp	2.5–10 µg/g FW
Cavendish banana	Fruit peel	100 µg/g FW
Potato (*Solanum tuberosum* var. *Desiree*)	Leaves	2–7 µg/g FW
Potato (*Solanum tuberosum* var. *Desiree*)	Tubers	< 0.5 µg/g FW
Portulaca (*Portulaca oleracea* L.)		39 µg/g DW
Ryegrass (*Lolium perenne* L.)	Seeds	37.66 µg/g FW
Cocoa (*Theobroma cacao*)	Been powder	1 µg/g FW
Broccoli (*Brassica olereacea* var. *italica*)		1 µg/g FW
Brousel sprouts (*Brassica olereacea* var. *gemmifera*)		1 µg/g FW
Oranges (*Citrus sinensis*)		< 1 µg/g FW
Tomatos (*Lycopersicon esculentum*)		< 1 µg/g FW
Aubergine (*Solanum melanogena*)		< 1 µg/g FW
Spinach (*Spinacia oleracea*)		< 1 µg/g FW
Beans (*Phaseolus vulgaris*)		< 1 µg/g FW
Peas (*Pisum sativum*)		< 1 µg/g FW
Apples (*Malus domestica* Borkh.)	ROOTS	5–6 ng/g FW
Apples (*Malus domestica* Borkh.)	Leaves	< 10 ng/g FW

3. Dopamine biosynthetic pathway

The biosynthetic pathways of catecholamines in plants (Figure 2) are similar to those in mammals. There are two pathways, and the precursor of both is tyrosine.[18,19] The first pathway starts with the decarboxylation of tyrosine by tyrosine decarboxylase (TYDC) to produce tyramine, which is then hydroxylated by monophenol hydroxylase (MH) to generate dopamine. The second pathway begins with the hydroxylation of tyrosine by tyrosine hydroxylase (TH) to produce levodopa (L-dopa), which is then decarboxylated by dopa decarboxylase (DD) to produce dopamine.[18,20] However, there is variability between the biosynthetic pathways for dopamine in different plants.

Indeed, the biosynthesis and catabolism of catecholamines have been described in several systems where differences can easily be identified. For example, tyrosine in *Musa sapientum* is first hydroxylated to form L-dopa, and then decarboxylated to form dopamine, while the synthesis of dopamine in cacti (*Opuntia stricta*) and purslane (*Portulaca oleracea* L.) initiated with the decarboxylation of tyrosine.[21] Furthermore, in the peyote cactus *Lophophora williamsii*, phenylalanine is hydroxylated to tyrosine, which is further hydroxylated to L-dopa or decarboxylated to tyramine.[22]

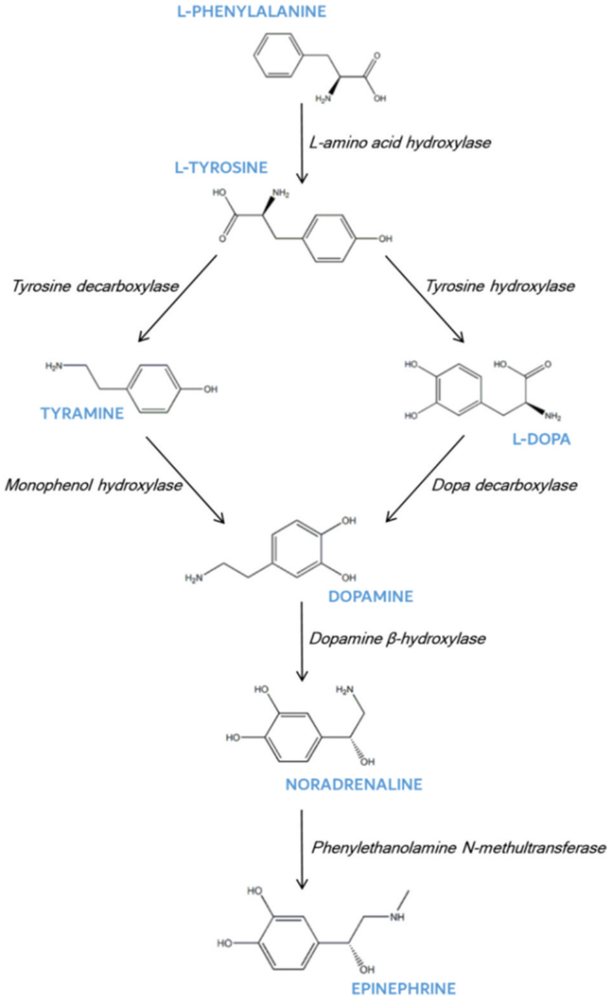

Figure 2. Dopamine biosynthetic pathways in plants.

In addition to variability in catecholamines biosynthetic pathways in plants, their synthesis is also influenced by environmental factors.[11] For example, the treatment of potato plants with abscisic acid (ABA) can increase the activity of TYDC, DD, and TH; high salt treatment increased the activity of TYDC; ultraviolet exposure increased the activity of DD; drought increased the activity of TH and DD; low-temperatures can reduce the activity of DD; and dark treatment and red light treatment can inhibit the activity of TYDC, TH, and DD.[11]

4. Plant growth and development

Some studies have suggested that catecholamines can interact with plant hormones. For example, treatment with ABA significantly increases the level of dopamine in potato plants.[23] The hormone GA3 induced hypocotyl elongation in lettuce seedlings,[24] and dopamine stimulated GA3 action in isolated lettuce hypocotyls.[25] Another study demonstrated that exogenous dopamine (5–100 μL) stimulated ethylene biosynthesis in illuminated chloroplast lamellae from sugar beet leaves.[26] In that study, dopamine was shown to function as a cofactor in reducing monovalent oxygen, which is necessary for the formation of ethylene. It is known that auxins promote the growth of stems and coleoptile while inhibiting the growth of roots.[27] The study by Kulma and Szopa showed that dopamine is key to the growth of lettuce hypocotyls,[1] which fits with the observation that dopamine inhibited oxidation of the auxin IAA by reducing the expression of IAA oxidase genes.[28] Catecholamines like dopamine are dihydroxyphenols, and biosynthetic dihydroxyphenols have been shown to inhibit IAA oxidase.[29,30] Thus, by inhibiting IAA oxidase in the roots, dopamine increases the auxin content, high levels of which can inhibit root growth. Therefore, this could be the mode of action by which dopamine inhibits root growth, as was observed in the growth of soybean seedling roots.[31]

Carbohydrate levels changed in plants that transformed with dopamine synthesis genes showed that dopamine are linked with sugar metabolism.[23] In previous study, overexpression of *TYDC* in potatoes increased the content of glucose and sucrose.[32] Increased expression of human dopamine receptor in potatoes resulted in increased sucrose, glucose, and fructose contents.[33] Apple plants pretreated with exogenous dopamine showed higher sucrose and malic acid contents but lower starch accumulation.[9] Gao et al. (2020) showed that exogenous dopamine increased the content of glucose and fructose by increasing the expression of sucrose phosphate synthase (*MdSPS1;6*), cell wall invertase (*MdCWINV1;2*) and neutral invertase (*MdCINV1;2*) in mycorrhizal plant under salt stress.[17]

In addition, the cyclic adenosine monophosphate (cAMP) signaling pathway, which participates in the regulation of numerous metabolic processes in the cell, can be regulated by catecholamines like dopamine. Through this interaction, dopamine has been associated with processes including nitrogen fixation, flowering, and the photophosphorylation of chloroplasts.[34,35] Protacio et al. (1992) showed that catecholamines stimulated growth in root cultures of *Acmella oppositifolia* and *Nicotiana tabacum*.[36] However, as noted previously, dopamine inhibited growth in soybean roots,[31] which may indicate that dopamine's promotion of plant growth is determined by plant-specific interactions with growth hormones.[37]

5. Abiotic and biotic stressors

5.1 Drought stress

The stress caused by drought is one of the most common abiotic stresses and has the greatest impact on crop yields.[38] Under drought conditions, plants usually close their stomata to minimize water loss, at the cost of reduced photosynthetic capacity.[11,39] In addition, drought directly affects the absorption of nutrients by plants,[40] which reduces growth rates and ultimately leads to a reduction in the accumulation of biomass.[41] A plant's water status can be observed by looking at indicators like relative water content (RWC), leaf water potential, osmotic potential, pressure potential, and transpiration rate,[42] all of which are significantly affected by drought. Drought stress can also lead to the production and accumulation of ROS (e.g.,$^{2-}$ O_2,$^{1}H_2O_2$, RO, and OH^-) in plants, which can have harmful effects.[11] The expression of the *TYDC* gene was induced in both *Arabidopsis* and *Malus hupehensis* by drought stress.[12,43] However, the effects of drought can be alleviated, the overexpression of *TH* can significantly increase the absorption and utilization of nutrients by plants, thereby improving their drought resistance.[43]

Dopamine can also reduce the impact of drought conditions by increasing the photosynthetic rates of plants. Dopamine was observed to increase the net photosynthetic rate in apple seedlings during drought conditions.[9] Furthermore, under drought conditions, plants pretreated with dopamine had higher intrinsic water-use efficiencies (WUE) than those that were not.[9] WUE is an important indicator of a plant's acclimation status to drought conditions and can determine its tolerance to drought.[44] Decreases in photosynthetic rate under drought conditions are related to disturbances to the photosynthetic pigments in leaves.[45] Exogenous dopamine significantly suppressed the upregulation of chlorophyll degradation gene (*PAO*) and senescence-associate gene (*SAG12*) under drought stress.[13] Studies have shown that dopamine increased Car, Chl a and Chl t content, keeping plants greener and reducing damage caused by drought.[9] Under drought, exogenous dopamine treatment can significantly improve the water retention capacity of apple leaves, reduce leaf wilt, reduce electrolyte extravasation and adjust stomatal opening.[9,11] It has been suggested that dopamine significantly increases the aperture size of the stomata under drought conditions.[11] Thus, by preventing the degradation of chlorophyll and adjusting stomata, dopamine is able to alleviate the negative effects of drought on photosynthetic capacity and reduce the impact of drought stress on plant growth.[11]

Dopamine can also improve the antioxidant capacity of plants. Studies have shown that dopamine can significantly limit increases of H_2O_2 in plant leaves caused by drought stress.[9] This may be related to increases in certain antioxidant enzymes like superoxide dismutase (SOD), peroxidase (POD), catalase (CAT), ascorbate peroxidase (APX) and glutathione reductase (GR) in the ascorbic acid-glutathione (ASA-GSH) circulation system of the leaves under drought conditions. The up-regulated expression of certain antioxidant genes like ascorbate peroxidase (*cAPX*), monodehydroascorbate reductase (*MDHAR*), dehydroascorbate reductase (*DHAR*) and glutathione reductase (*cGR*) may also contribute to the antioxidant capacity.[46,47] The strong antioxidant effect of dopamine is believed to be mainly due to: (a) Dopamine's direct antioxidant capability. Studies have shown that dopamine's antioxidant capacity is equal to ascorbic acid's and catechin's, which have strong antioxidant capacities.[48] (b) Melanin, the oxidation product of dopamine, is a strong active oxygen scavenger.[49] (c) Exogenous dopamine treatment can activate the antioxidant system of plants, thereby indirectly removing reactive oxygen species.[9]

5.2 Salt stress

Under salt stress, plants usually close or constrict their stomata to prevent water loss.[50] However, closing stomata also restricts entry of CO_2 to the leaf cells, thereby inhibiting photosynthesis.[51] These methods of reducing the impact of salt stress can also disrupt the ion homeostasis within plants.[12] The restricted ion exchange can lead to the formation of superoxide, hydrogen peroxide, hydroxyl radicals, singlet oxygen, and other ROS.[52] When subjected to salt stress, the activities of the antioxidant enzymes CAT, APX, POD, and SOD in plants increase, and the degree of the increase is related to the salt tolerance of the plant.[52] Furthermore, from observed increases in activity of tyrosine hydroxylase in potato tubers under salt stress, we know that salt stress can induce dopamine synthesis.[32]

As discussed, exogenous dopamine treatment alleviated chlorophyll degradation and improved photosynthesis under salt stress.[12,53] Dopamine can reduce the content of Chl b, and in so doing increase the Chl a/b ratio and prevent the accumulation of excess of electrons, which is an adaptive mechanism in the photosynthetic electron transport chain.[54] Studies have shown that exogenous dopamine can increase the degree to which stomata are opened, increasing the length and width of stomata in plants under salt stress. With dopamine treatment, the maximum stomatal openings of *Malus* were under 100 μM.[14] Studies have shown that sugar and ABA can regulate stomatal behavior under different environmental scenarios and other studies have shown that dopamine can regulate sugar metabolism and ABA content. This may be the pathway by which dopamine is able to regulate plant stomatal behavior under salt stress.[1] Dopamine has also been shown to regulate the expression of the rice aquaporin gene *OsPIP1-3* under salt stress.[55] It has been observed that treatment of cucumber seedlings with dopamine prior to the induction of nitrate stress inhibited the negative effects on plants by increasing the carbon metabolism, nitrogen metabolism-related enzymes and the expression of related genes.[53]

Under salt stress, Na^+ and K^+ concentrations in leaves can be important indicators of plant salt tolerance. The application of exogenous dopamine can significantly inhibit the absorption of Na^+ by plants while maintaining high levels of K^+ content.[12] Studies have also found that exogenous dopamine can improve the water-use efficiency of plants under salt stress.[12] Higher WUE can reduce the plant's intake of salt and prevent a water deficit.[56] It is believed that plant cells under salt stress can reduce the concentration of Na^+ in the cells by expelling them or compartmentalizing them into vacuoles, thereby lessening the impact of the salty conditions.[57] Studies have also shown that the application of exogenous dopamine can increase the expression of Na^+/H^+ antiporter genes (*MdHKT1, MdNHX1, MdSOS1, MdSOS2*, and *MdSOS3*) in the roots and leaves of apple plants under salt stress, thereby maintaining a higher K^+/Na^+ ratio within plants and alleviating the damage caused by salt stress.[12]

The application of dopamine can improve the antioxidant capacity of plants under salt stress by increasing the activities of SOD, POD, CAT, and APX and inhibiting the production of H_2O_2.[12,58,59] The ASA-GSH cycle plays an important role in the salt tolerance of plants. Studies have found that the application of exogenous dopamine can significantly enhance the activities of plant dehydroascorbate reductase (DHAR) and monodehydroascorbate reductase (MDHAR) under salt stress. It has also been shown that dopamine can regulate the photosynthetic oxygen reduction process.[48,52] The protective effect of dopamine on plants under salt stress may be attributed to its ability to act as a natural medium for chemical analogs and to act as an oxygen reduction factor, enabling oxygen reduction to participate in energy conversion during photosynthesis.[48] Therefore, dopamine can exert an important protective effect on plants under salt stress by preventing oxidative stress-induced tissue damage at the cellular level.[60,61]

5.3 Nutrient stress

Nutrient deficiencies can significantly reduce photosynthetic rates in plants as well as reduce the concentrations of photosynthetic pigments.[11,12] Nutrient stress reduces the photosynthesis rate of plants because, when nutrients are deficient, the synthesis of biological components required for photosynthesis can be halted, which can reduce the efficiency of photosynthesis or disrupt it altogether.[62] The root system is the first organ to be affected by changes in the nutrient content of the soil, so the growth status and configuration of the root system are important indicators of a plants ability to obtain nutrients.[63,64] Under nutrient-deficient conditions, plant roots will adapt by continuously adjusting their physiological and structural characteristics, and the degree to which they can adapt depends on their ability to change the root architecture.[65] The effects of nutrient deficiencies on plant roots manifest mainly in reductions in root length, diameter, volume, surface area, quantity, and number of root hairs.[11,66] Throughout the life cycle of a plant, the realization of optimal physiological function requires a stable supply of nutrients, with a nutrient deficiency the normal growth of plants will be affected and plant biomass will be reduced.[67] Furthermore, under nutrient stress the ASA-GSH circulatory system, which is an important pathway for ROS removal, can be altered, potentially reducing ROS removal efficiency.[11,12]

Dopamine alleviated the inhibitory effect of nutrient stress on plant photosynthesis, probably by regulating certain physiological and biochemical processes related to photosynthesis.[12] It has been shown that dopamine can be used as an analog of naturally occurring substances that regulate the process of oxygen reduction in spinach photosynthesis.[1] In addition, dopamine can alleviate the inhibitory effects of nutrient stress on photosynthetic rates by adjusting leaf stomatal conductance to improve the utilization of CO_2 and by maintaining high concentrations of chlorophyll.[12] Similarly, dopamine can alleviate the inhibitory effect of nutrient deficiency on the absorption and accumulation of large and trace elements.[12] The root structure of plants is determined according to nutrient availability to best maximize absorption and utilization.[63] The effect of dopamine on element absorption when nutrients are lacking is related to its ability to alter the root configuration. For example, under potassium-deficient conditions, apples were able to reconfigure their roots, like changing the length and diameter of their roots, to enhance potassium absorption and utilization.[12] In addition to influencing root structure, exogenous dopamine treatment can enhance the transfer of nutrients from the roots to stems and leaves, and increase nutrient accumulation in roots. Therefore, dopamine can enhance the adaptability of plants to nutrient stress by regulating the absorption of nutrients by plants and their transfer and distribution within plants. Studies also have shown that exogenous dopamine can scavenge ROS by up-regulating the expression of ASA-GSH cycle-related genes, thereby improving resistance to nutrient stress.[11]

5.4 Plant diseases

Numerous studies have shown that the biosynthesis of hydroxycinnamic acid amides from tyramine, and their subsequent polymerization in the cell wall by oxidative enzymes, are an integral component of a plant's response to a pathogen challenge.[68,69] These amides, together with other cell wall-bound phenolics, are believed to create a barrier against pathogens by reducing the digestibility of the cell wall.[70] Several reports have suggested that TYDC is involved in the biosynthesis of numerous secondary metabolites and thus also contributes to the plant immune response against infection.[68,71] Notably, tyramine, the product of dopamine, can effectively restrict sexual reproduction and inhibit the growth of fungal hyphae.[72] Therefore, it has been suggested that dopamine plays a role in disease resistance. Indeed, the expression of the *TYDC* gene has been shown to be higher in disease-resistant plants than in susceptible plants.[73] In one case, the *TYDC* gene from parsley was introduced into potatoes to catalyze the metabolism of tyrosine, this increased the tyramine content in the cell wall and effectively improved the disease resistance of the potatoes.[74] Similarly, introducing the poppy *TYDC* gene into rapeseed significantly improved the binding of tyramine to the cell wall and reduced the digestibility of cells.[70] Studies have shown that *TYDC* expression can be induced by pathogenic bacteria as well as by methyl jasmonate,[75] and that it participates in the biosynthesis of hydroxyphenylacrylamide. As a component of the cell wall, amides are considered a physical barrier against pathogens, so an increase in cell-wall amides can contribute to an increase in disease resistance.[70,71]

6. Conclusions and future prospects

Dopamine is a type of catecholamine which emerged as a multifunctional ubiquitous signaling molecule. In this review, we discussed the dopamine biosynthesis pathway and summarized the most relevant aspects concerning abiotic and biotic stressors (Figure 3). The expression of dopamine biosynthesis genes can be induced by drought, salt, and diseases, which may lead to an increase of endogenous dopamine content in plant (Figure 3a). Dopamine involved in plant growth and development, and against several abiotic stresses by affecting stress-related genes expression, such as chlorophyll degradation, senescence, nitrate transport, IAA oxidase, aquaporin, and carbohydrate related genes (Figure 3c; Table 2). Endogenous or exogenously applied dopamine alleviated the damage to plants caused by many abiotic and biotic stresses (Figure 3b).

However, there are numerous vital issues that need to be elucidated in the future. Genes involved in dopamine biosynthesis and metabolism pathway in plants remain to be further clarified. Many studies have focused on the application of exogenous dopamine to plants and the effects of increasing endogenous dopamine through transgenic methods need to be more thoroughly explored. In addition, the study of catecholamine receptors is helpful to reveal the mechanism of it at the molecular level. Dopamine receptors in plants have not been reported. However, many experiments have shown the existence of plant catecholamine receptors. Verelst et al. (2004) have identified a class of DoH-CB proteins in plants that can

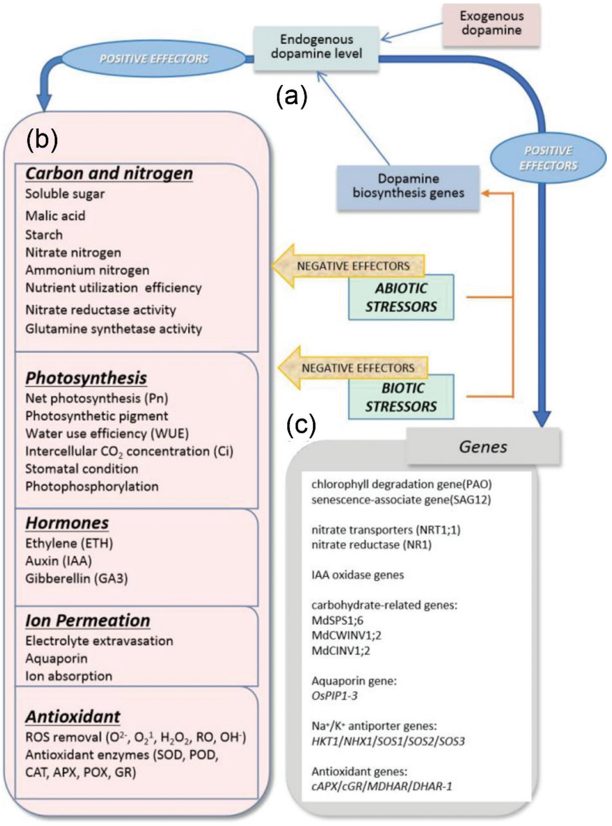

Figure 3. Schematic of dopamine's positive effects on physiological processes. Abiotic and biotic stressors provoke an increase into endogenous dopamine level through the upregulation of dopamine biosynthetic genes (panel A). Stressors act as negative effectors in many physiological processes such as carbon and nitrogen metabolism, photosynthesis, and hormone levels (panel B). Endogenous dopamine can regulate the expression of many genes and regulatory factors, which can reduce the negative effects of biotic/abiotic stressors on physiological processes (panels C).

Table 2. Dopamine biosynthesis genes and related genes regulated by dopamine in plants.

	Gene names
Dopamine biosynthetic genes	L-amino acid hydroxylase Tyrosine decarboxylase Tyrosine hydroxylase Monophenol hydroxylase Dopa decarboxylase
Dopamine metabolism genes	Dopamine β-hydroxylase Phenylethanolamine N-methultransferase
Leaf Senescence	Chlorophyll degradation gene (*PAO*) Senescence-associate gene (*SAG12*)
Carbohydrate metabolism	Sucrose phosphate synthase (*MdSPS1*) Malate dehydrogenase (*MdMDH*) Malic enzyme (*MdME*) Aldose-6-phosphate reductase (*MdA6PR*) Sorbitol dehydrogenase(*MdSDH1*) Cell wall invertase (*MdCWINV1*)
Salt overly sensitive (SOS) pathway	*MdSOS1* *MdSOS2* *MdSOS3* *MdHKT1* *MdNHX1*
Nitrate transporters	*CsNRT1.1* *CsNR1.*
Antioxidant genes	*cAPX* *cGR* *MDHAR* *DHAR-1*
Aquaporin gene	*OsPIP1* *OsPIP2* *OsPIP3*
IAA	IAA oxidase genes

regulate the activity of catecholamines.[76] DoH-CB protein can bind to dopamine through the induction of auxin. It is speculated that DoH-CB protein may be the receptor of plant catecholamines, and the binding between them is induced by auxin.[77] To conclude, dopamine increase plant stress resistance is a new field that needs further study, but may provide useful clues for the cultivation of new plant varieties resistant to stress.

Disclosure of potential conflicts of interest

No potential conflicts of interest were disclosed.

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