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Research Progress on the Effect of Exogenous Additives Treatment on the Synthesis of Plant Secondary Metabolites

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Abstract: Plant secondary metabolites play an important role in plants' response to environmental changes and stress conditions. Exogenous additives such as plant hormones, chemical elicitors, and natural extracts can significantly affect the synthesis and function of these secondary metabolites by regulating gene expression and signal transduction pathways, providing new strategies for enhancing plant stress resistance and optimizing the production of secondary metabolites. This study reviews the effects of exogenous additives on the synthesis of plant secondary metabolites, including plant hormones, ion stress, and their synergistic effects with environmental factors. Exogenous additives significantly affect the types and contents of secondary metabolites by regulating metabolic pathways, activating defense mechanisms, and optimizing metabolic networks. In addition, the combined application of different exogenous additives and their synergistic effects with environmental factors can effectively improve plant stress resistance and optimize the production of secondary metabolites. The study suggests that future research should further develop and apply new exogenous elicitors and strengthen the study of their potential side effects and long-term impacts to achieve sustainable optimization of secondary metabolite production. It also provides important technical support for the development and processing of functional foods, helping to produce food products with higher nutritional value and health benefits.

Keywords: Plant secondary metabolites; Exogenous additives; Plant hormones.

1. Introduction

Plant secondary metabolites are a variety of chemical substances produced by plants in response to environmental changes and stress conditions. These substances play a crucial role in ecological defense, signal transduction, and the interaction between plants and the environment. In recent years, with the continuous progress of biotechnology and phytochemistry, researchers have gradually recognized the crucial role of exogenous additives in regulating the synthesis of plant secondary metabolites. Exogenous additives such as plant hormones, chemical elicitors, and natural extracts can significantly affect the types, contents, and physiological functions of secondary metabolites by regulating gene expression and signal transduction pathways, providing new strategies for enhancing plant stress resistance and optimizing the production of secondary metabolites [1].

Although exogenous additives show broad application prospects in regulating the synthesis of plant secondary metabolites, their specific action mechanisms and application effects in different plants still need to be further studied. The development of modern analytical techniques, such as high-performance liquid chromatography-mass spectrometry (HPLC-MS), provides strong support for the accurate detection and quantitative analysis of secondary metabolites in plants, laying the foundation for revealing the action mechanisms of exogenous additives [2]. However, the effects of different exogenous additives on secondary metabolites vary depending on many factors such as plant species, additive types, and their concentrations. Therefore, in-depth exploration of the interactions of these factors is of great significance for further optimizing the application of exogenous additives.

2. Overview of Plant Secondary Metabolites and Exogenous Additives

2.1. Definition and Classification of Plant Secondary Metabolites

Plant secondary metabolites refer to the chemical substances produced by plants in addition to primary metabolism. These compounds do not directly participate in plant growth, development, and reproduction, but are essential for plant survival and adaptation to the environment. Secondary metabolites include many chemical classes, mainly including alkaloids, flavonoids, flavones, phenolic compounds, terpenoids, and organic acids. Among them, flavones and flavonoids are widely distributed in plants and have strong antioxidant properties, which can be used in food development, especially in the development of functional foods, such as anti-inflammatory, antioxidant, and cardiovascular protection functions; some other secondary metabolites, such as terpenoids, are not only beneficial to the development of functional foods but also play a key role in the ecological defense of plants, protecting plants from pathogens, insects, and other biological threats [3]. In addition, some phenolic compounds play an important role in signal transduction and the interaction between plants and the environment, helping plants adapt to and respond to external environmental changes.

2.2. Definition and Classification of Exogenous Additives

Exogenous additives refer to external chemical substances that are artificially applied to plants and can affect the physiological and biochemical processes of plants. Studies have pointed out that exogenous additives can be divided into many types such as plant hormones, chemical elicitors, and natural extracts. These substances affect the synthesis of secondary metabolites by regulating the hormone balance in plants and activating or inhibiting specific metabolic pathways [4]. Plant hormones, as a type of exogenous additive, can significantly affect plant growth and development and the synthesis of secondary metabolites by changing gene expression patterns and signal transduction pathways. Especially in enhancing stress resistance and increasing the yield of secondary metabolites, the role of plant hormones is particularly significant [5].

2.3. Mechanism of Exogenous Additives Affecting Plant Secondary Metabolites

The mechanism by which exogenous additives affect the synthesis of plant secondary metabolites is complex and diverse, mainly acting through multiple levels such as regulating signal transduction pathways, gene expression, and enzymatic reactions in plants. Exogenous plant hormones such as jasmonic acid (JA) and salicylic acid (SA) can act as signal molecules to mediate plants' response to environmental stress, thereby inducing the synthesis of secondary metabolites. These hormones activate a series of signal transduction pathways, such as the MAPK cascade reaction, regulate the expression of key enzyme genes related to the synthesis of secondary metabolites, and then increase the accumulation of secondary metabolites in plants. Especially when plants are attacked by pathogens or under environmental stress, exogenous additives can quickly activate the defense response of plants and significantly enhance the antioxidant activity and disease resistance of secondary metabolites [5].

In addition, exogenous additives also regulate the synthesis of secondary metabolites by affecting the flow of metabolic pathways in plants. For example, exogenous hormones can indirectly affect the metabolic pathways of secondary metabolites by regulating the balance of endogenous hormones such as ethylene and abscisic acid (ABA) in plants. These additives can change the biosynthesis pathways of secondary metabolites, promote the accumulation of certain specific metabolites, and inhibit the synthesis of other metabolites [6]. In addition, with the development of plant metabolomics, the application of advanced analytical methods such as high-performance liquid chromatography-mass spectrometry enables researchers to more accurately track the impact of exogenous additives on the synthesis pathways of secondary metabolites, providing strong technical support for further revealing their action mechanisms [7]. Through in-depth research on the action mechanisms of exogenous additives, scientific basis can be provided for the application of these additives in agricultural production to improve crop resistance and the yield of secondary metabolites.

3. Effect of Plant Hormones on the Synthesis of Secondary Metabolites

3.1. Gibberellin (GA)

Gibberellin is one of the important endogenous hormones in plants, which mainly promotes plant growth and development by regulating cell elongation, division, and differentiation. Hedden P et al. [8] pointed out that GA promotes the synthesis of α-amylase during plant growth, enhancing the decomposition of starch in endosperm cells and providing energy for seed germination. In addition, GA also regulates the expression of downstream genes by activating GA-dependent transcription factors, thereby controlling plant morphogenesis and organ development. Experimental data show that under GA treatment, the plant height of rice increased by about 25%, and the development of the root system also showed a significant enhancement. These research results indicate that GA plays a crucial role in plant growth and development, especially in regulating the auxin signal pathway in plants, and its synergistic effect with auxin significantly affects the growth rate and morphogenesis of plants.

Gibberellin not only plays an important role in promoting plant growth but also affects the synthesis of specific secondary metabolites by regulating secondary metabolic pathways. Zhang J et al. [9] found that GA can disrupt the balance of endogenous hormones in plants, thereby inhibiting the synthesis of certain secondary metabolites. In Pseudostellaria heterophylla, GA inhibits the synthesis of abscisic acid, resulting in a significant decrease in the accumulation of flavonoids. Li W et al. [10] found that GA not only promotes the development of lily flowers but also indirectly controls the synthesis of secondary metabolites by affecting the transcriptional regulatory network related to secondary metabolism. CHEN X et al. [11] cloned the Ca2+-ATPase gene and studied its function in the GA-dependent signal pathway, and found that the expression of this gene is regulated by GA, which in turn affects the synthesis of plant secondary metabolites. Specifically, GA regulates the activity of key enzymes in the secondary metabolism in plants through this signal pathway, thereby controlling the synthesis and accumulation of certain important metabolites. ALLA M M N et al. [12] found that GA can significantly improve the stress resistance of Vigna sinensis and Zea mays by regulating the balance of intracellular signal transduction and secondary metabolic pathways. Data analysis shows that after GA treatment, the content of these secondary metabolites increased by about 20 - 35%, further verifying the important role of GA in plants' response to adversity.

CHEN X C et al. [13] investigated the effect of GA on the transcriptome of grape flowers and found that GA can induce changes in the expression of a series of genes related to secondary metabolism, thereby affecting the synthesis of secondary metabolites. WANG C H et al. [14] further revealed the role of GA in regulating the synthesis of artemisinin, a secondary metabolite in Artemisia annua. Experimental results show that after GA treatment, the yield of artemisinin decreased by about 40%, indicating that the regulatory role of GA in the synthesis of secondary metabolites may be closely related to the expression of the DXR gene. LIANG Z et al. [15] studied the interaction between GA and other plant hormones such as abscisic acid and ethylene on the synthesis of phenolic acids in the hairy roots of Salvia miltiorrhiza. The study found that GA treatment can regulate the synthesis of secondary metabolites in Salvia miltiorrhiza, especially the production of phenolic acids, through synergistic interaction with ABA and ethylene signal pathways. Experimental data show that after GA treatment, the content of phenolic acids increased by about 50%. This finding indicates that the role of GA in secondary metabolism regulation is not only reflected in individual regulation but also further complicates its regulatory mechanism through interaction with other hormones.

3.2. Methyl Jasmonate (MeJA)

Methyl jasmonate is an important signal molecule in plants and plays a key role in plant defense responses. Todd A T et al. [16] found that MeJA can regulate the synthesis of alkaloids in the secondary metabolic pathways of plants by activating a series of transcription factors. These transcription factors, such as WRKY and MYC2, can interact with inhibitors (such as JAZ proteins) in the jasmonate signal pathway, thereby promoting the expression of defense-related genes. GE Q et al. [17] revealed the regulatory role of MeJA in the jasmonate signal pathway of Salvia miltiorrhiza through combined transcriptomic and metabolomic analysis. They found that the JAZ inhibitor controls the synthesis pathway of secondary metabolites through interaction with the jasmonate signal molecule. Especially after MeJA treatment, the content of salvianolic acid B in Salvia miltiorrhiza significantly increased. Experimental data show that the content of salvianolic acid B increased by approximately 50%. TU L et al. [18] focused on the regulation of the synthesis of triterpenoids by the jasmonate signal pathway in Tripterygium wilfordii. They identified the cytochrome P450 gene family involved in the biosynthesis of triterpenoids through whole-genome sequencing and functional gene analysis, and found that these genes were significantly upregulated after MeJA treatment, thereby promoting the synthesis of the anticancer active ingredient triptolide in Tripterygium wilfordii. Experimental data show that after MeJA treatment, the content of triptolide increased by about 60%, demonstrating the important role of MeJA in the regulation of plant secondary metabolism.

Zhao Yujun et al. [19] further studied the effect of MeJA on the expression of the squalene synthase gene and found that MeJA can significantly upregulate the expression of this gene, thereby improving the synthesis efficiency of triterpenoids in Tripterygium wilfordii. Experimental data show that MeJA treatment increased the expression level of the SQS gene by approximately 2 times, thereby promoting the synthesis of the secondary metabolite triptolide, and the content increased by about 50%. CARETTO S et al. [21] studied the effect of MeJA and miconazole on the synthesis of artemisinin in Artemisia annua cell suspension cultures and found that MeJA treatment can significantly increase the yield of artemisinin, especially when combined with miconazole, the content of artemisinin increased by about 70%. In addition, gene expression analysis showed that MeJA treatment activated multiple genes related to artemisinin synthesis, including members of the cycloartenol synthase and cytochrome P450 gene families. These findings indicate that MeJA significantly regulates the synthesis of plant secondary metabolites by activating specific metabolic pathways.

KIM Y S et al. [22] found that in Centella asiatica cells, MeJA treatment can significantly promote the synthesis of triterpenoids by upregulating the expression of the squalene synthase gene. Experimental data show that after MeJA treatment, the contents of asiatic acid and madecassic acid increased by about 2.5 times and 2 times, respectively, indicating the importance of MeJA in regulating the synthesis of triterpenoids and revealing its broad application potential in the biosynthesis of secondary metabolites. Andi SA et al. [23] investigated the effect of combined treatment of MeJA and phenylalanine on the synthesis of secondary metabolites in grape cell suspension cultures through research. They found that MeJA treatment can significantly increase the synthesis of flavonoids and phenolic compounds. Experimental data show that the contents of these secondary metabolites increased by about 55%. Wei Q et al. [24] revealed the regulatory mechanism of MeJA on the biosynthesis of terpenoids in Curcuma wenyujin. They found through transcriptomic analysis that MeJA treatment induced the upregulated expression of multiple genes related to terpenoid synthesis, including terpene synthase and cytochrome P450 family members. Experimental data show that after MeJA treatment, the content of curcumin increased by about 65%, indicating the key role of MeJA in regulating the synthesis of terpenoid metabolites. Yue X et al. [25] studied the effect of exogenous sucrose and MeJA on the synthesis of monoterpenoids in grapes and found that MeJA treatment significantly increased the accumulation of monoterpenoids in grapes, especially when combined with sucrose, the content of monoterpenoids increased by about 3 times. Transcriptomic analysis showed that MeJA treatment activated multiple metabolic pathways related to secondary metabolism, especially the expression of key genes in the terpenoid synthesis pathway.

3.3. Salicylic Acid (SA)

Salicylic acid plays a crucial role in plant immune responses, especially in the establishment of systemic acquired resistance. Jirakiattikul Y et al. [26] found that SA can enhance the resistance of plants to pathogens by activating the expression of plant defense genes. In the tissue culture of banana, SA treatment significantly increased the accumulation of secondary metabolites in plants, especially the contents of phenolic compounds and flavonoids related to disease resistance. Singh S [26] found that SA can significantly improve the antioxidant activity of spinach leaves by inducing the accumulation of phenolic substances. Experimental data show that after SA treatment, the total phenolic content in spinach leaves increased by about 50%, and the activities of antioxidant enzymes such as superoxide dismutase and catalase also significantly increased. Hasanuzzaman M et al. [27] found that in rice and wheat, the antioxidant enzyme activity increased by about 40% after SA treatment, which significantly improved the tolerance of plants to salt and drought stress. In addition, SA also enhances the stress resistance of plants by regulating the synthesis of defensive secondary metabolites, such as flavonoids and terpenoids.

3.4. Cytokinins (CKs)

Cytokinins mainly regulate cell division and differentiation and also play an important role in the synthesis of plant secondary metabolites. Liu Changzhou et al. [28] pointed out that CKs activate a series of genes related to the cell cycle through signal transduction pathways, thereby promoting the division and proliferation of plant cells. In addition, CKs can also affect the synthesis of certain important metabolites by regulating secondary metabolic pathways, especially in plant tissue culture and callus induction. Experimental data show that under CKs treatment, the induction rate of plant callus increased by about 20%, and the accumulation of secondary metabolites also significantly increased. Song Jinping [29] found in the tissue culture of Taxus chinensis that CKs not only promoted the proliferation of plant tissues but also significantly affected the synthesis of the secondary metabolite paclitaxel. Experimental results show that appropriate concentration of CKs treatment increased the yield of paclitaxel by about 30%, indicating the important role of CKs in regulating the synthesis of secondary metabolites.

Zhu Hongwei et al. [30] found that CKs can significantly enhance the synthesis of flavonoids and terpenoids in callus by promoting cell division and enlarging cell volume. Experimental data show that after CKs treatment, the content of flavonoids in callus increased by about 25%, and the content of terpenoids increased by about 15%, indicating the broad application potential of CKs in the synthesis of secondary metabolites. Cheng Yupeng et al. [31] found in the study of callus induction of Bupleurum scorzonerifolium that CKs not only significantly increased the growth rate of callus during the induction of callus formation but also promoted the accumulation of saikosaponins by regulating genes related to the synthesis of secondary metabolites. YAHIA A et al. [32] revealed the synergistic effect of CKs and ethylene in Catharanthus roseus cell suspension culture. They found that CKs play an important role in the synthesis of secondary metabolites by stimulating the synthesis of indole alkaloids in plants. Especially, CKs and ethylene jointly promote the accumulation of these secondary metabolites through two different mechanisms. Experimental data show that CKs treatment increased the content of indole alkaloids by about 50%, demonstrating the importance of CKs in the regulation of plant secondary metabolism.

3.5. Ethylene

Ethylene, as a key gaseous hormone in plants, is involved in multiple physiological processes from seed germination to fruit ripening. Chen Y F et al. [33] explored the molecular mechanism of ethylene signal transduction and emphasized that ethylene activates the expression of downstream genes through the EIN2/EIN3 pathway, thereby regulating plant growth and development and secondary metabolism. Woeste K E et al. [34] found that the loss-of-function mutant RAN1 in the ethylene response pathway exhibits growth abnormalities that may be caused by excessive activation of the ethylene signal, such as the lethal rosette leaf phenotype. These studies indicate that ethylene signal transduction needs to be precisely regulated to ensure the normal development of plants and avoid the negative effects caused by excessive signal activation.

Ethylene also plays an important role in the short-term growth response of plants, especially in rapid environmental stress responses. Binder B M et al. [35] found that ethylene regulates the short-term growth response of Arabidopsis seedlings through an EIN3/EIL1-independent pathway. This indicates that ethylene not only plays a role in long-term developmental processes but can also quickly respond to environmental changes and affect the physiological response of plants through short-term mechanisms. In addition, ethylene also plays a complex role in the synthesis of secondary metabolites. Fits L et al. [38, 39] pointed out that ethylene and jasmonic acid jointly regulate the expression of secondary metabolism genes, especially playing a synergistic role in plant stress resistance and the accumulation of secondary metabolites.

Ethylene not only affects plant growth and development through direct signal transduction but also has a dual regulatory effect on the synthesis of secondary metabolites. Fang Rongjun et al. [40] found that ethylene can enhance the resistance of plants to pathogens by regulating the secondary metabolic pathways related to defense responses. However, ethylene may also reduce the accumulation of certain compounds by inhibiting certain secondary metabolite synthesis pathways. This dual effect indicates that ethylene has a complex and diverse role in the regulation of secondary metabolite synthesis, and the specific effect depends on plant species, environmental conditions, and the interaction with other hormones.

3.6. Abscisic Acid (ABA)

Abscisic acid, as an important member of plant hormones, is mainly involved in the response of plants to abiotic stress and also plays a key role in regulating the synthesis of plant secondary metabolites. Zhen Mengyuan et al. [41] pointed out that ABA promotes the biosynthesis of certain secondary metabolites, such as flavonoids and terpenoids, by regulating the expression of key genes related to secondary metabolism. These secondary metabolites not only contribute significantly to plant stress resistance but also have important medicinal value. Experimental data show that under ABA treatment, the content of certain secondary metabolites increased by about 30%, indicating the significant role of ABA in the regulation of plant secondary metabolism. Yoshida T et al. [42] explored the role of ABA-dependent and ABA-independent signal pathways in plants' response to osmotic stress and emphasized the mechanism by which ABA enhances plant resistance by regulating the synthesis of secondary metabolites under stress conditions. The study found that ABA treatment can activate defense genes related to osmotic stress, thereby promoting the accumulation of secondary metabolites, such as flavonoids in the phenylalanine ammonia-lyase pathway. The increase in this metabolite helps plants survive and adapt in harsh environments.

Abscisic acid not only plays a role in plants' response to environmental stress but also has a profound impact on plant physiological processes by regulating the synthesis pathways of specific secondary metabolites[47-51]. Jing F et al. [47] found that ABA treatment can significantly increase the content of artemisinin in Artemisia annua mainly by enhancing the expression of key genes in the artemisinin biosynthesis pathway. Experimental data show that after ABA treatment, the content of artemisinin increased by about 40%, providing new possibilities for the application of ABA in the production of secondary metabolites in medicinal plants. Zhang Rui et al. [52] further investigated the effect of different concentrations of ABA on the accumulation of terpenoid secondary metabolites in Tripterygium wilfordii suspension cells. The study found that with the increase in ABA concentration, the content of terpenoids in Tripterygium wilfordii also showed a significant increase. Especially under high concentration ABA treatment, the accumulation of terpenoids increased by about 50%. This research result indicates that ABA regulates the synthesis of secondary metabolites through a concentration-dependent mechanism and has a significant regulatory effect on the accumulation of secondary metabolites. Kageyama A et al. [50] revealed the special role of ABA in the synthesis of secondary metabolites in bryophytes. They found that in the liverwort Marchantia polymorpha, ABA treatment can induce the biosynthesis of bibenzyls and enhance the tolerance of plants to ultraviolet C (UV-C). Experimental data show that after ABA treatment, the content of bibenzyls increased by about 45%, indicating the potential of ABA in improving plant tolerance to environmental stress and its unique role in the synthesis of secondary metabolites in different plants.

4. Effect of Ion Stress on the Synthesis of Secondary Metabolites

4.1. Calcium Ion (Ca^{2+})

Calcium ion (Ca^{2+}) is an important signal molecule in plants and is widely involved in regulating plant growth and development and secondary metabolic responses. Kumar S et al. [53] pointed out that calcium signal plays a key defensive role in plants facing biotic stress by regulating the activity of a series of transcription factors and enzymes. Fluctuations in calcium ion concentration can activate calcium-dependent protein kinases in plant cells, and these kinases regulate the expression of downstream genes through phosphorylation, thereby promoting the synthesis of secondary metabolites. Li Y et al. [54] further emphasized that calcium signal not only plays a role in response to biotic stress but also regulates the accumulation process of plant secondary metabolites. For example, under specific environmental conditions, calcium ion can affect the types and contents of secondary metabolites through signal transduction pathways, enhancing plant stress resistance and medicinal value.

The regulatory mechanism of calcium ion in plant secondary metabolism is manifested in its ability to respond to the internal environment and external stimuli of plants. González-Hernández AI et al. [55] found that exogenous calcium treatment can significantly affect the development of tomato roots and regulate the synthesis of secondary metabolites through the calcium signal pathway. This regulatory mechanism involves the activation of the calcium-dependent signal pathway, thereby regulating the expression of genes related to secondary metabolism. Studies have shown that exogenous calcium application increased the content of secondary metabolites in tomato roots by about 20%, demonstrating the important role of calcium ion in secondary metabolism regulation. Fan Zhantao et al. [56] further explored the mechanism of calcium ion in the growth and secondary metabolite accumulation of medicinal plants. The study pointed out that calcium ion affects the response of plants to external stress by regulating the stability of cell membranes and the structure of cell walls, thereby promoting the accumulation of secondary metabolites. For example, calcium ion significantly increases the medicinal value of plants by enhancing the synthesis of flavonoids and saponins in medicinal plants. Experimental data show that after calcium ion treatment, the content of secondary metabolites in certain medicinal plants increased by about 30% to 40%. Luo Shihong et al. [57] revealed the regulatory role of calcium ion on the metabolic activities in the special structures of plants by studying the secondary metabolites in these structures. They found that calcium ion can enhance the resistance of plants to environmental stress by regulating the secondary metabolic pathways in special structures such as root hairs and leaf epidermis. Under the regulation of calcium ion, these special structures can significantly increase the accumulation of secondary metabolites, such as terpenoids and phenylpropanoids. These research results indicate that calcium ion not only plays a regulatory role in the overall synthesis of plant secondary metabolites but also functions importantly in specific tissues and cell structures, providing a new perspective for in-depth understanding of the mechanism of calcium signal in secondary metabolism regulation.

4.2. Sodium Ion (Na^+) Stress

Sodium ion (Na^+), as the main component of salt stress, has a wide range of effects on the physiological processes of plants. Salt stress can cause changes in the osmotic pressure of plant cells, triggering a series of physiological reactions, such as decreased stability of cell membranes, ion imbalance, and reduced photosynthetic efficiency. Anjitha KS et al. [58] found that salt stress disrupts the water balance in plants by increasing the Na^+ content in plants, leading to cell dehydration and metabolic disorders. Shahverdi MA et al. [58] studied the response of Stevia rebaudiana to NaCl stress and found that the accumulation of Na^+ significantly inhibits plant growth and leads to a decrease in photosynthetic pigment content, directly affecting photosynthesis and energy production. Khare T et al. [60] further pointed out that the combined action of Na^+ and Cl^- exacerbates the physiological stress of plants, especially showing significant negative effects on the proline metabolism and nitrosative response in rice (Oryza sativa), ultimately leading to growth stagnation and a decrease in biological yield.

Sodium ion (Na^+) stress not only affects the basic physiological processes of plants but also significantly regulates the synthesis of plant secondary metabolites. Anjitha KS et al. [58] pointed out that secondary metabolites play a key role in metal stress tolerance, and Na^+ stress affects the types and contents of secondary metabolites by changing the ion balance and metabolic pathways in plants. For example, Na^+ stress can induce the synthesis of certain antioxident enzymes and defense-related metabolites to help plants resist the oxidative stress caused by salt stress. Shahverdi MA et al. [59] found in the study of Stevia rebaudiana that Na^+ stress significantly affects the accumulation of diterpene glycosides, especially the contents of stevioside and rebaudioside A are reduced under high salt conditions. Experimental data show that under NaCl stress, the contents of these secondary metabolites decreased by about 25%, indicating that Na^+ stress affects the normal synthesis of metabolites by inhibiting the activity of key enzymes in the secondary metabolic pathway. Shi Pengjie et al. [61] revealed the effect of sodium ions on the retention behavior of alkaloids in plants. They found that sodium ions can change the solubility and stability of certain alkaloids in plants, thereby affecting their accumulation and distribution in plant tissues. Specifically, alkylsulfonate ions have a significant effect on the retention behavior of alkaloids in Areca catechu. Experimental data show that under specific concentrations of sodium ion treatment, the content of alkaloids increased by about 15% to 20%, indicating the complex mechanism of Na^+ in regulating the synthesis and accumulation of plant secondary metabolites.

4.3. Other Important Ion Stress Factors

Other ions such as magnesium ion (Mg^{2+}), iron ion (Fe^{2+}), and heavy metal ions (such as copper ion Cu^{2+} and aluminum ion Al^{3+}) also have significant effects on the synthesis of plant secondary metabolites. Anjitha KS et al. [58] pointed out that metal ion stress significantly affects plant metabolic pathways and the accumulation of secondary metabolites by inducing oxidative stress and changing ion balance. Zhan X et al. [63] found that environmental and genetic factors jointly regulate the biosynthesis of secondary metabolites, and heavy metal ions affect the yield and types of secondary metabolites by binding to key enzymes in plants and inhibiting or activating specific metabolic pathways. Sanclemente MA et al. [64] found that sugar modulation can relieve the stress of heavy metal ions on plants in some cases, thereby maintaining the normal metabolic function of plants. These studies indicate that ion stress has a complex and multi-level mechanism in the regulation of plant secondary metabolism and requires further in-depth research to fully understand its specific effects in different plant systems.

5. Comprehensive Effect and Interactive Influence of Exogenous Additive Treatment

The combined application of exogenous additives shows significant advantages in enhancing the synthesis effect of plant secondary metabolites. Through synergistic effects, exogenous additives can simultaneously activate multiple metabolic pathways, thereby significantly increasing the accumulation of specific secondary metabolites [65]. For example, in the hairy root culture of Lysimachia christinae, the combined use of multiple exogenous additives significantly increased the content of anti-inflammatory components, and in the treatment of tomato fruits, the combined use of 5-aminolevulinic acid and other additives not only increased the pigment content but also improved the fruit quality [66, 67].

The synergistic effect of exogenous additives and environmental factors also plays an important role in the regulation of the synthesis of plant secondary metabolites. Environmental conditions such as temperature, light, and water, in combination with exogenous additives, can enhance the stress resistance and defense ability of plants by regulating their secondary metabolic pathways, thereby better coping with biotic and abiotic stresses [67,68]. This synergistic effect can effectively stimulate the defense mechanism of plants, delay leaf senescence, maintain normal physiological functions, and further enhance the survival ability of plants in adverse environments [69, 70].

In addition, exogenous additives further optimize the production of plant secondary metabolites by overall regulating the metabolic network. Studies have shown that exogenous additives can enhance the activity of the phenylpropanoid and nitrogen metabolism pathways in plants, thereby significantly increasing the contents of flavonoids and amino acids [71]. This regulatory effect is particularly significant in the production of secondary metabolites in medicinal plants, and through the comprehensive analysis of transcriptomics and metabolomics, the regulatory mechanism of exogenous additives at the molecular level is further revealed [72].

These studies not only reveal the complex regulatory role of exogenous additives on plant secondary metabolism under different environmental conditions but also provide new ideas and application prospects for the development of functional foods [73, 74]. By precisely controlling the types, concentrations, and interactions of exogenous additives with environmental factors, the contents of secondary metabolites beneficial to human health, such as flavonoids, carotenoids, and polyphenols, in plants can be significantly increased, thereby promoting the production of efficient and natural functional foods [75-77]. These studies not only contribute to the development of functional foods rich in antioxidants, anti-inflammatory substances, and other health-promoting ingredients but also provide the possibility of customized food products that meet the unique nutritional needs of specific populations. For example, for the prevention and management of chronic diseases such as cardiovascular diseases, diabetes, and cancer, through the precise application of exogenous additives, functional foods with special therapeutic effects can be designed, thereby improving people's quality of life [78, 79].

6. Conclusion and Outlook

In summary, exogenous additives have shown broad application prospects in regulating the synthesis of plant secondary metabolites, especially in enhancing plant stress resistance and optimizing the production of secondary metabolites. Different types of exogenous additives significantly affect the types and contents of plant secondary metabolites by regulating gene expression, signal transduction pathways, and metabolic networks. However, currently, research is still insufficient to fully reveal the specific regulatory role of exogenous additives on plant secondary metabolism under different environmental conditions, which poses a challenge to understanding their application potential under biotic and abiotic stress conditions. Although some studies have explored the effects of exogenous additives, research on the possible metabolic imbalances and potential side effects is still limited.

In the future, research should pay more attention to the practical application value of these exogenous additives in food processing and the development of functional foods. By deeply revealing how exogenous additives affect the synthesis of plant secondary metabolites through molecular regulatory mechanisms, more accurate guidance can be provided for the development of functional foods, especially in improving the nutritional value and health functions of foods. In addition, the comprehensive analysis of transcriptomics and metabolomics will help clarify the specific regulatory pathways and action modes of these additives at the molecular level, thereby optimizing the production process of functional foods and improving their market competitiveness. Through the continuous development and application of new exogenous elicitors, the food processing industry in the future will be able to better utilize plant secondary metabolites to produce more health-promoting foods, meet consumers' demand for healthy diets, and promote the continuous innovation and development of the functional food industry.

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