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Bioassay of Root Exudates, their Impact in Susceptible Species and their Degradation in Hydroponics: A Review

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Authors' contributions

This work was carried out in collaboration among all authors. All authors read and approved the final manuscript.

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Review Article

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ABSTRACT

Plants grown in hydroponics exhibit superior characters and yield compared to those grown in soil. However, root exudates accumulated particularly in renewed nutrient solution (RNS) hinders development of crops in hydroponics. These exudates are secondary metabolites released by the roots as a result of physiological processes, exhibiting autotoxic effects in plants. They are allelochemicals encompassing various chemical groups such as phenolic compounds, terpenoids, alkaloids, benzoxazinoids or other organic acids. The quantity and type of allelochemical released by plants varies depending on multiple factors such as temperature, light, nutrient deficiency, stress, physiological status of plant, pH and environment. The combined effect of more than one allelochemical is often additive or synergistic thus elevating the impact caused by individual allelochemical. These phytotoxic exudates are known to have inhibited the growth and development

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of plants by diverse pathways unique to their characteristic. There are several methods developed for degradation of exudates including AC (Activated Charcoal), O_3/H_2O_2 treatment or other. This review discusses the bioassay of secondary metabolites causing autotoxicity, mechanism, impact in horticultural and ornamental crops, factors affecting their release and methods for elimination in hydroponics.

Keywords: Root exudates; allelochemicals; degradation; autotoxic; renewed nutrient solution.

1. INTRODUCTION

"Allelopathy is a common biological phenomenon by which one organism produces biochemicals that influence the growth, survival, development, and reproduction of other organisms" [1]. "The allelopathic interactions involve inhibitory influence of a plant on growth and development of neighboring plants belonging to same species (autotoxicity) or different species (heterotoxicity) due to the chemicals exuded from any part of the allelopathic plant. The degree of allelopathy depends on disease, nutrition, insects, competition , biotic factors such as nutrients level, and abiotic factors such as temperature, irradiation, draught, and pH" (Cseke & Kaufman 2006) [2]. "Autotoxicity refers to the form of intraspecific allelopathy wherein biochemicals released from plants of one species significantly hinders or suppress the overall development of same species. These biochemicals released are termed as allelochemicals. Allelochemicals are non-nutritional secondary metabolites which are released by plants in different conditions and processes" [3]. "Root extracts and exudations are the common sources of allelochemicals with potent biological activity and are produced by numerous plant species, with great variation in chemical components" [4]. "Allelochemicals range from simple hydrocarbon to complex polycyclic aromatic compounds like phenol, flavonoids, tannins, steroids, amino acids, alkaloids and quinones" [5]. "There are several factors reported to cause autotoxicity in plants. According to a report, the effect of autotoxicity becomes more pronounced when plants are cultivated on the same soil for years or grown in recycled hydroponic solutions for several cultures" [6]. "Recycling nutrient hydroponic solution by addition or altering the nutrient concentration in closed hydroponics system can induce building up of certain minerals which are not absorbed at the same rate as the minerals added along which contributes to autotoxicity. According to research, besides sulfates, chlorides and bicarbonates also have a tendency to accumulate, and can influence crop growth" [7]. "It been reported to occur in a number of crop plants in agroecosystem causing serious problems such as growth reduction, yield decline and replant failures" [8]. "This inhibitory biochemical interaction among plants of same species is induced by the combined action of toxic biochemicals released into the surrounding environment. Current evidence indicates allelopathic inhibition most often results from the combined action of several different chemicals according to which a specific allelochemical may be present at a concentration below its growth inhibition threshold and still affect growth by several combinations of allelochemicals [9]. Autotoxicity phenomenon in hydroponics is studied in several vegetable crops such as cucumber (*Cucumis sativus*), taro (*Colocasia esculenta*), some leafy vegetables, strawberry and ornamentals such as African marigold" [10]. Several methods have been investigated to eliminate phytotoxic root exudates from hydroponics nutrient solution such as addition of activated charcoal, auxin treatment, microbial strain, electrodegradation, LEDs, supplementation of amino acids, membrane filtration and others. These exudates play crucial role in plant growth when present in suitable range and thus understanding more about root exudates can help grow crops sustainably in hydroponics with greater yield and quality growth. This article aims to conclude the bioassay of biochemicals causing autotoxicity in hydroponically grown crops, their impact and mechanism, factors influencing their mode of action, their combined impact on development of crop and potential measures for their elimination.

2. BIOASSAY OF ALLELOCHEMICALS CAUSING AUTOTOXICITY AND THEIR MECHANISM

"The compounds released from plant roots are known to have either stimulatory or inhibitory effect on growth of same plant species or on other species grown in vicinity both in hydroponics and in soil. Allelochemicals are plant secondary metabolites, compounds considered nonessential for the direct development of cells, released into the environment *via* root exudation, leaching by precipitation, volatilization, or decomposition of plant tissues" [11]. "Plants grown in closed hydroponics system have been reported to accumulate secondary metabolites that hinder normal physiological functioning and plant growth. Allelochemicals detected in nutrient solution of hydroponically grown crops variably belong to phenolic acids, terpenoids, organic acids, flavonoids or are derivatives of various secondary metabolites released. Among various groups of allelochemicals, terpenoids and phenols are majorly responsible for autotoxicity in many crop species. Allelopathic inhibition typically results from a combination of allelochemicals which interfere with several physiological processes in the receiving plant or microorganism" [12]. "Activity of compounds within a particular class can be quite different and sensitivity among species and in the numerous bioassay systems varies a great deal" [12]. Allelopathic compounds can be distinctly categorised into different groups based on structure and mechanism. Major allelochemicals include phenolic compounds, alkaloids, terpenoids or hydroxamic acids of benzoxazinoids.

Table 1. Categorisation of allelochemicals and their mechanism in plants

Major Allelochemical Groups	**Allelochemicals**	**Mechanism**	**Reference**
Phenolic allelochemicals (-OH group)	aromatic phenols, hydroxy and substituted benzoic acids and aldehydes, hydroxy and substituted cinnamic acids, coumarins, tannins, and perhaps a few of the flavonoids	Changes in cell membrane permeability and inhibition of plant nutrient uptake; inhibition of cell division and elongation; reduce the chlorophyll content; weakened oxygen absorption capacity; effects various enzyme functions; reduce the physiological activity of plant hormones; inhibition of protein synthesis	Li et al*.,* 2010 [13]
Alkaloid allelochemicals	indole alkaloids from tryptophan, pyrrolizidine alkaloids from ornithine or arginine, and quinolizidine alkaloids from lysine	Interference with DNA, enzymatic activity, protein biosynthesis and membrane integrity in developing plants.	Parida and Deb 2023 [14]
Terpenoids $(C5H8)_n$	volatile monoterpenoids, such as alpha-pinene, camphor, 1,4-cineole and 1,8-cineole; sesquiterpene lactones (cynaropicrin, cynaratriol, desacylcynaropicrin, and 11,13-dihydrodesacylcynaropicrin) a, monoterpene menthol, sesquiterpene artemisinin, diterpene paclitaxel, triterpene ginsenoside and tetraterpene carotenoid	inhibiting plant growth, affecting the function of cell membrane and hindering the physiological metabolism, interference with enzyme activity, aberrant development in shoots, affecting all phases of mitosis	Huang et al*.,* 2021 [15] Parida and Deb 2023 [14]
Hydroxamic acids of Benzoxazinoids	2,4-dihydroxy-1,4-benzoxazin-3-one (DIBOA) and 2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3-one (DIMBOA)	Disruption of photosynthesis is an important and frequently observed physiological effect of benzoxazinoids.Benzoxazolin2-one (BOA) has been shown to induce changes in leaf water relations, photosynthesis and carbon isotope discrimination in lettuce (Lactuca sativa)	Parida and Deb 2023 [14] Hussain et al. [16]

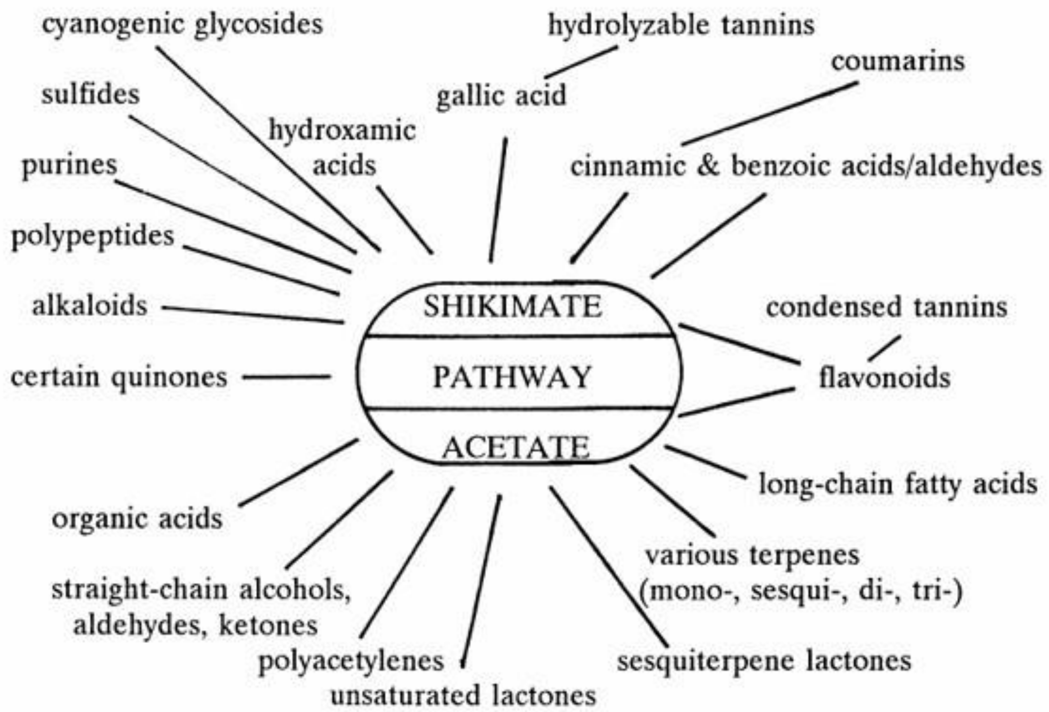

Fig. 1. Some of the diversity of allelochemicals implicated in allelopathy. The sketch does not list all classes of allelochemicals and is not intended to show amino acid intermediates or other pathway details [14]

3. IMPACT OF METABOLITES ON PLANT GROWTH

"These metabolites have been found to affect various physical processes during plant growth and development, including inhibition of seed germination, photosynthesis, respiration, root growth, and nutrient uptake, with diverse mechanisms involving cell destruction, oxidative homeostasis and photoinhibition" [5]. "For instance, in closed hydroponic systems, strawberry roots release phenolic acids, mainly benzoic acid, into the culture solution inhibits the growth and metabolic activities of strawberry roots" [6]. "On the contrary, allelochemicals are potentially the stimulator of beneficial responses in plants at low concentration. For instance, studies showed that low concentrations (below 10^{-3} M) of caffeic acid (CA) promoted the hypocotyl elongation of lettuce (*Lactuca sativa*) seedlings, but higher concentrations inhibited seedling growth and seed germination" [5]. "The mechanism of allelochemicals affecting plant roots also involves cellular structure modifications and oxidation system" [5]. "The effect of several allelochemicals when present together is known to be additive or synergistic. The joint action of 50 micro-M each of ten benzoic acid allelochemicals was generally as inhibitory to the growth of velvetleaf (*Abutilon theophrasti*) as 500 micro-M of a single compound" [12]. However, the additive impact of individual biochemical in combined effect of several allelochemicals remains a curious mystery.

4. FACTORS AFFECTING EXUDATION OF ALLELOCHEMICALS

Allelochemicals are released by plants in response to stress conditions as defense mechanism. Abiotic factors such as temperature, pH imbalance, light exposure, drought stress or nutrient deficiency thus dominantly control the quantity and type of allelochemical released. It has been reported that abiotic stresses cause increased release of allelochemicals to the surrounding environment. Further research hints at passive leakage of allelochemicals as exudates. "The regulatory release of exudations continues to be a debatable discussion as the substances released by plants cannot be isolated from the tissue. Inhibitory *p*-benzoquinones, known as sorgoleone, are abundant in *Sorghum* root exudates but have not been found in the root tissues" [17]. "Abiotic factors largely interfere with the enzymatic activity inside plants. A previous study revealed that in *Cucumis sativa*, the concentration of benzoic acid (i.e., a major allelochemical) exuded by the roots increase in nutrient solutions with increasing temperature and photoperiod length" [18]. "Increased root exudation of carboxylates (e.g., citrate, malate, oxalate) is a P- deficiency response and enhanced leakiness of membranes in response to P deprivation may also contribute to enhanced release of sugars, amino acids and organic acids" [17]. "Diffusion mediated release of root exudates is likely to be affected by root zone temperature due to temperature-dependent changes in the speed of diffusion processes and modifications of membrane permeability" [17]. "A decrease of exudation rates at low temperatures may be predicted for exudation processes that depend on metabolic energy" [17]. "Since a large proportion of organic carbon released into rhizosphere is derived from photosynthesis, changes in light intensity are likely to modify the intensity of root exudation" [19]. Biotic factors are vaguely acknowledged as the cause for stimulation of root exudates release in hydroponics but some reports hint at elevated levels of toxic compounds in hydroponics nutrient solution for plants with any injury or those infected with disease causing organisms.

Table 2. Impact of allelochemicals in horticultural and ornamental crops with possible degradation method

CROP	Allelochemical	Degradation method	Impact	References
Beans • *Phaseolus vulgaris* • *Vicia faba*	○ Benzoic*, salicylic*, and malonic acid* ○ lactic, benzoic*, *p*-hydroxybenzoic, vanillic, adipic*, succinic, malic, glycolic*, and *p*-hydroxyphenylacetic acid*	➢ Electrodegradation method ➢ Application of AC (Activated Carbon)	In ***Phaseolus vulgaris***, number of leaves, maximum leaf width, shoot fresh mass, and shoot dry mass were significantly reduced to 67, 83, 78, and 84% compared with those of the control, respectively, at 50 micro M concentration of benzoic acid. Salicylic and malonic acids decreased the number of leaves, shoot fresh mass, and shoot dry mass compared with those of the control. In ***Vicia faba***, shoot length, fresh mass, and transpiration rates were affected by salicylic acid at concentrations higher than 3.5 micro M. benzoic acid at 50 micro M significantly reduced root length, and shoots fresh and dry mass to 89, 83, and 81% those of the control, respectively. Adipic	Asaduzzaman and Asao (2012) [8]

CROP	Allelochemical	Degradation method	Impact	References
			and p-hydroxyphenylacetic acids decreased root length to 87 and 88% of that of the control, respec-tively.	
Strawberry	○ Methyl esters of lactic, benzoic*, succinic, adipic and p-hydroxybenzoic acids	➢ Activated Charcoal addition ➢ Electrodegradation of root exudates ➢ Auxin Supplementation ➢ Supplementation of Amino acids or LEDs ➢ Benzoic acid degrading bacteria ➢ Application of GA3, Si, and UV/H2O2	Increased electrolyte levels in cells and root lipid peroxidation; decreased free radical scavenging activity of roots; abnormal mineral and water uptake. Significant reduction in root length. Autotoxic condition discolors the roots from brown to black and ultimately destroy them completely. These damaged roots are unable to uptake water and mineral nutrients from the nutrient solution and as a result, growth retardation occurs. Significant decrease in number of flowers per plant and number of fruits per plant.	Talukder et al. (2019) [20] Asaduzzaman and Asao (2020) [6] Asao and Asaduzzaman (2012) [21]
Leafy vegetables • Taro • Lettuce • Parsley • Celery	○ lactic acid, benzoic acid*, *m*-hydroxybenzoic acid, *p*-hydroxybenzoic acid, vanillic acid, succinic acid and adipic acid ○ Pisatin, lactic, benzoic acid*, *p*-hydroxybenzoic, vanillic*, succinic and adipic acid ○ lactic, benzoic*, *p*-hydroxybenzoic acid, adipic* and succinic acid ○ lactic*, benzoic* and *p*-hydroxybenzoica cid	➢ Adsorption by AC ➢ Electrodegradation ➢ Benzoic acid degrading bacteria	**Taro-** Soot growth retardation, lower leaf count, decreased corm yield per plant and Adipic acid reduced dry weight of roots. **Lettuce-** Vanillic acid caused severe growth inhibition in curly-leaf lettuce. **Parsley-** Adipic acid induced the retardation of dry weight of parsley shoots. **Celery-** Lactic acid in celery reduced dry weight of shoots.	Asao et al. (2003) [22] Asao et al. (2004) [23]
Tomato	○ Benzoic*,	➢ Addition of (Activated	Increased carbon	Yu and Matsui

CROP	Allelochemical	Degradation method	Impact	References
	palmitic, phthalic vanillic, cytokinins, 4-hydroxybenzoic* and gentisic acid	Charcoal). ➢ Addition of Benzoic acid degrading bacteria	concentration in the solution due to accumulation of organic exudates from the roots or their secondary products by microbes. Uptake of P by the roots of tomato was inhibited by phenolic acids. The length and TTC-reducing activity of the root of tomato seedlings were decreased. Decrease of the TTC-reducing activity caused a decrease in energy production, followed by a decrease in nutrient uptake.	(1993) [24] Yu et al. (1993) [25]
Cucumber	○ 2,4-dichlorobenzoic acid (DCBA)* ○ Cinnamic Acid Derivatives	➢ Application of epibrassino-lide ➢ DCBA-degrading microorganism (microbial strain)	Inhibitory effect on growth of cucumber seedlings in early stage. Decreased yield of cucumber plants in the late reproductive stage and shrunken fruits.	Asao and Asaduzzaman (2012) [10] Asaduzzaman and Asao (2020) [6] Asao et al. (2004) [23]
Ornamentals • **Pot marigold** • **Bishop's weed** • **Lily** • **Prairie gentian** • **Snapdragon**	○ lactic, succinic and benzoic acid* ○ Lactic acid ○ n-Caproic, benzoic, *p*-Hydroxybenzoic, adipic acid and vanillin ○ malonic, maleic, n-Caproic, benzoic, malic, *m*-Hydroxybenzoic and *p*-Hydroxybenzoic acid ○ n-Caproic acid	➢ Electrodegradation is the most efficient method for benzoic acid degradation. ➢ Application of AC.	Plant length, number of leaves and flowers per plant, root length, and plant dry weight almost all decline in ornamental crops due to the Autotoxic effect. Lactic acid significantly reduce fresh shoot weight and root dry weight in pot marigold even at low concentration. Benzoic and p-hydroxybenzoic acid in lily, even at 50 μM, significantly reduce root fresh weight.	Asao and Asaduzzaman (2012) [10]

5. DEGRADATION OF ROOT EXUDATES IN HYDROPONICS

In closed hydroponics system, root exudates accumulate in the nutrient solution thus inhibiting growth. Reused nutrient solution (RNS) is primarily responsible for autotoxicity in hydroponics due to non- removal of exuded biochemicals. For effective growth of plants inside hydroponics, it is imperative to supply nutrients in desired quantities as well as removing toxic substances. As discussed earlier, these toxic compounds belong to various groups and their release depend on certain factors, therefore, it is crucial to not just concentrate on removal of these biochemical exudates but to maintain appropriate growth conditions to prevent release of allelochemicals from plants. Several methodologies have been developed for degradation of exudates inside hydroponics culture which involve addition of activated charcoal, electrodegradation, supplementation of amino acids, microbial degradation and others. The effect of activated charcoal on growth of crops such as lettuce, tomato, strawberry etc in hydroponics has been studied by many researchers. It has been concluded that porous surface of activated charcoal adsorbs the phytotoxic substances from the nutrient solution and has been investigated to decrease the carbon concentrations resulting from organic exudates. According to research, in tomato, the dry weight of the lamina, fruits, and whole plant, together with the fruit yield, for the cultivation with activated charcoal was about 1.2 times that in the case of cultivation without activated charcoal [25]. However, activated charcoal is not always effective in removal of all types of phytotoxic compounds. High-dose activated carbon treatment could not eliminate the harmful impact of these phytotoxic substances on plant growth [26]. Ion exchange resins in general, and weakly basic ion exchange resin in particular, could also be used for removal of organic acids from aqueous streams containing low concentrations [27]. Weak base resins are useful in removal of selective compounds excreted at low concentrations. Another technique is the use of electrodegradation method to significantly reduce the concentration of benzoic acid in the nutrient solution and increase the yield of strawberry, but the operation of this method is complicated and the investment is high [20]. The use of electrodegradation method in non-renewed nutrient solution for lettuce growth is effective in maintaining oxidative damage caused to lettuce plants by the action of allelochemicals such as benzoic, phenyl acetic, cinnamic, p-hydroxybenzoic, lauric, phthalic, vanillic, palmitic, and stearic acids etc thereby, regulating the mineral uptake and normal metabolism [20]. The most potent inhibitor among phytotoxic exudates is benzoic acid which is known to inhibit growth and other vital plant processes at lowest concentration. It was investigated that O_3 treatment alone is not suitable for removing benzoic acid from the nutrient solution of lettuce grown hydroponics; O_3/ H_2O_2 treatment is effective for mitigating autotoxicity and degrading benzoic acid [28]. Microbial degradation of allelochemicals is another effective method which involves use of microbial strains belonging to different genotypes for successful elimination of phytochemicals. Phenolic acid-degrading bacterium V4, a member of the genus *Sphingobium*, referred to as *Sphingobium* sp. V4 has been revealed to effectively degrade vanillic acid, ferulic acid, *p*-coumaric acid, *p*-hydroxybenzoic acid, and syringic acid under a wide range of abiotic factors [29]. The efficacy of various other methods are being investigated for elimination of major allelochemical groups released as exudates from roots of wide variety of crops grown in hydroponics [30,31].

6. CONCLUSION

In conclusion, accumulation of the secondary metabolites poses significant challenge for crop growth in hydroponics. A better understanding of release of phytotoxic chemicals in plants is essential for developing a sustainable methodology in crop production using renewed nutrient solution in hydroponics. Furthermore, studying the effect of root exudates on plant-microbe interactions could provide information for improving positive interactions and boosting plant health in hydroponic conditions.

COMPETING INTERESTS

Authors have declared that no competing interests exist.

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