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Review

Autotoxicity in Strawberry Under Recycled Hydroponics and Its Mitigation Methods

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Strawberry plants are grown in hydroponics for higher quality and yield, as this system excludes soil-borne disease issues. Recycled hydroponics is practiced to make cultivation cost-effective, sustainable, and environmentally friendly. However, due to recycling of hydroponic nutrient solution, plant root exudates accumulate, leading to autotoxicity, a form of allelopathy that inhibits growth and development. In recent decades, commercial cultivation of strawberry under greenhouse and plant factory conditions following recycled hydroponics has been widely adopted globally. Subsequently, yield decline has also been reported due to development of autotoxicity from the accumulated root exudates. In recycled hydroponic systems, strawberry plant growth is inhibited by root exudates that contain mainly phenolic acids in the culture solution. In this regard, elimination of these accumulated root exudates or allelochemicals from the culture solution would restore inhibited plant growth and yield. A number of research studies have been conducted on autotoxicity in strawberry and possible mitigation methods. These studies suggested that addition of activated charcoal in the nutrient solution, supplementation of auxin on leaves, electro-degradation of root exudates in nutrient solution, and supplementation of amino acids and/or LEDs can effectively remove/degrade/mitigate autotoxicity in strawberry grown under recycling hydroponics. This review mainly discusses the autotoxicity phenomenon in strawberry under recycled hydroponics, the responsible allelochemicals and their mechanism of action, mitigation methods and future research endeavors in this field.

Key Words: activated charcoal, amino acids, electro-degradation, *Fragaria* × *ananassa* Duch., LED lights.

Introduction

Autotoxicity is a form of allelopathy that occurs within plant species through the release of a variety of phytotoxic chemicals which cause growth inhibition (Rice, 1984; Putnam, 1985; Singh et al., 1999). This phenomenon happens when accumulation of root exudates exceeds toxic levels due to continuous recycling of the hydroponic nutrient solution (Yu et al., 1993; Asao et al., 2003; Kitazawa et al., 2005; Asaduzzaman and Asao, 2012). 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 (Takahashi, 1984; Zhao et al., 2015). In greenhouse and plant factory vegetable production, nutrient solution is usually recycled to make efficient use of valuable fertilizers and also to reduce environment pollution (Yang and Zhang, 2005; Kozai, 2013; Hosseinzadeh et al., 2017). The exudated chemicals responsible for inhibition of plant growth and development are known as allelochemicals, autotoxic chemicals or simply phytotoxins. These released allelochemicals are either secondary metabolites or the waste products of the primary metabolic processes of plants. They are diverse in nature including different organic acids, fatty acids, phenolic acids, tannins, terpenoids, amino acids, polypeptides, alkaloids, and nucleotides, etc. (Gross and Parthier, 1994; Einhellig, 1995; Rice, 1995; Seigler, 1996).

In agricultural ecosystems, release of these allelochemicals from the plant happens via several natural processes such as leachation from living and/or dead plant parts (Overland, 1966), root exudation (Tang and Young, 1982; Yu and Matsui, 1994, 1999; Asao et al., 2003, 2004a, b; Kitazawa et al., 2005; Chen et al., 2011; Asaduzzaman and Asao, 2012), decomposition of residues, and volatilization from the plant organs (Rice,

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1974, 1984; Petrova, 1977; Singh and Kohli, 1992; Einhellig, 1995; Inderjit, 1996; Kohli et al., 1997). In recycled hydroponics, root exudates are common sources of potentially bioactive allelochemicals (Inderjit and Weston, 2003). In fact, they are one of the main sources of plant chemicals released into the rhizosphere that are responsible for chemical interference in plants. Research results indicated that synthesis and exudation of allelochemicals are mainly boosted by both biotic and abiotic stress conditions, including extreme temperatures, droughts, and exposure to UV light (Inderjit and Weston, 2003).

Under stress conditions, roots release ions, as well as oxygen and water, but root exudates mainly consist of carbon-containing compounds (Uren, 2000). Plants produce several different types of root exudates either as mixtures of compounds with no appropriate function, or as mixtures with some known function, such as lubrication. Root excretions are thought to be involved in regulation of the internal metabolic processes of the plant, such as respiration and nutrient acquisition. Although roots produce nearly every major type of compound found in plants, they generally do not produce chlorophyll or specific compounds related to photosynthesis. The amount of root exudates varies by plant species, cultivar, age, and stress factors (Uren, 2000). Roots also exude a variety of low-molecular weight organic compounds including sugars and simple polysaccharides, amino acids, organic acids, and phenolic compounds. Some of these compounds, especially the phenolics, influence the growth and development of surrounding plants and soil microorganisms. In addition, higher-molecular-weight compounds such as flavonoids, enzymes, fatty acids, growth regulators, nucleotides, tannins, carbohydrates, steroids, terpenoids, alkaloids, polyacetylenes, and vitamins are also released in large quantities (Rovira, 1969; Hale et al., 1978; Curl and Truelove, 1986; Fan et al., 1997; Uren, 2000).

In the commercial hydroponic production of strawberry run out is often allowed once used culture solutions enter the surrounding environment and cause pollution. Recycling of the culture solution under closed hydroponics can be sustainable and economical, but at the same time may lead to the development of autotoxicity as a result of accumulated allelochemicals from root exudates. In closed hydroponic systems, strawberry roots release phenolic acids, mainly benzoic acid, into the culture solution (Kitazawa et al., 2005). The accumulation of root exudates in the culture solution inhibits the growth and metabolic activities of strawberry roots. This ultimately causes electrolyte levels in cells and root lipid peroxidation activities to increase, and free radical scavenging activity of roots to decrease (Zhen et al., 2003). Additionally, the damaged strawberry roots exhibit abnormal uptake of water and mineral nutrients from the culture solution. Consequently, shoot and root growth, the number of flowers and harvested fruits per plant, and fruit development are adversely affected (Kitazawa et al., 2005).

Growth and yield of strawberry under autotoxicity can be improved by the renewal of used nutrient solution at certain interval, but this leads to a waste of resources, time and labor. In this regard, recycling hydroponics causes accumulation of root exudates or allelochemicals has a crucial flaw that hampers sustainable productivity under protected cultivation systems. In recent years, researchers have found several effective methods to eliminate growth inhibitors from recycling hydroponic cultivation systems, such as adding activated charcoal to the nutrient solution (Kitazawa et al., 2005), supplementation of auxin (Kitazawa et al., 2007), electro-degradation of root exudate in the nutrient solution (Asao et al., 2008; Asaduzzaman et al., 2012; Talukder et al., 2019), supplementation of amino acids (Mondal et al., 2013) and supplementation with amino acids and LEDs (Talukder et al., 2018). The present review discusses the autotoxicity phenomenon in strawberry, its occurrence under recycled hydroponics, the responsible allelochemicals and their mechanism of action and also mitigation options.

Autotoxicity and Allelochemicals from Root Exudates of Strawberry under Recycled Hydroponics

Autotoxicity has been observed in both natural and managed cultivation systems. Plant roots and their exudates, bark, tissues, and also volatiles can cause autotoxicity and a number of studied have been reported in alfalfa (Miller et al., 1988; Dornbos et al., 1990; Chung et al., 2000; Chon et al., 2002), asparagus (Hartung et al., 1990; Miller et al., 1991), apple (Börner, 1959), cucumber (Yu and Matsui, 1994), eggplant (Chen et al., 2011), lettuce (Asao et al., 2004a, b; Lee et al., 2006), broad bean and pea (Asaduzzaman and Asao, 2012), taro (Asao et al., 2003), tomato (Yu and Matsui, 1993), and strawberry (Kitazawa et al., 2005).

In greenhouses and plant factories, commercial strawberry growers use closed hydroponic cultivation systems for sustainable vegetable and ornamental plant production (Takeuchi, 2000; Oka, 2002). However, the closed hydroponics culture technique is characterized by the problem of autotoxicity due to continuous accumulation of allelochemicals in the culture solution (Asao et al., 2003, 2007; Kitazawa et al., 2005). Strawberry plants develop autotoxicity under recycled hydroponics and thereafter growth parameters such as number of leaves, shoot sand root biomass decrease, as well as a decrease in the number of flowers and fruits per plant. Root exudates in the culture solution can be trapped by activated charcoal and subsequent extraction and analysis confirmed benzoic acid as being the most damaging potential allelochemical in strawberry (Kitazawa et al., 2005). In other studies, it has been reported that growth and metabolism of strawberry roots were inhibited due to accumulation of exudates in the growth medium, leading to an increase in percentages of cell electrolytes, a decrease in free radical scavenging activity, and an increase in root lipid peroxidation (Zhen et al., 2003). Consequently, an autotoxic condition discolors the roots from brown to black and ultimately destroys them completely. These damaged roots are unable to uptake water and mineral nutrients from the nutrient solution and as a result, growth retardation occurs (Kitazawa et al., 2005). In other studies, it was suggested that the coordination of hydroxybenzoic acid and *F. oxysporum* showed an elevated negative effect on the degree of inhibition of leaf photosynthesis in strawberry (Zhao et al., 2009). The long-term continuous cropping of strawberry may also lead to unfavorable rhizosphere soil conditions for bacterial community diversity (Li et al., 2018). Further research was recommended to determine how the quality of soil was reduced by the shift in the diversity of the soil bacterial community.

A collected root exudate fraction showed the presence of phytotoxic chemicals at considerable levels in the recycled hydroponic solution. Root exudates could be removed by adding activated charcoal to the nutrient solution (Koda et al., 1977; Asao et al., 1998, 1999a; Sato, 2004). In later studies Kitazawa et al. (2005) investigated the effects of non-renewed nutrient solution, and addition of activated charcoal to the nutrient solution, on vegetative and reproductive growth of strawberry. Activated charcoal has been used to trap strawberry root exudates and then desorbed and extracted following the method described by Pramanik et al. (2001) and Yu and Matsui (1993). GC-MS and HPLC have been the most popular instruments used to identify autotoxins from different parts of plant. The autotoxic chemicals from the root exudates of strawberry have been detected by gas chromatography coupled with a mass spectrometer (GC-MS), showing more than 20 peaks (Fig. 1; Kitazawa et al., 2005) and the potential identified allelochemicals include lactic acid, benzoic acid, succinic acid, adipic acid and *p*-hydroxybenzoic acid. In other studies, strawberry allelochemicals, mainly phenolic acids, were identified from the decomposing residues from a continuous cropping field (Zhen et al., 2004; Tian et al., 2015) and also from replanting soil of different cultivars (Zhao et al., 2012; Cao et al., 2016).

Mechanism of Action of Allelochemicals from Strawberry Root Exudates

When plants experience autotoxicity they release allelochemicals to the rhizosphere through various means and mechanisms. Exposure to these allelochemicals leads to various ecological and physiological negative effects (as shown the schematic diagram in Fig. 2; Weir et al., 2004) on plant growth (Rice, 1984), mineral uptake (Lyu and Blum, 1990; Baziramakenga et al., 1994), membrane permeability (Baziramakenga et al., 1995), stomatal closure and water stress (Barkosky and Einhellig, 1993), respiration (Penuelas et al., 1996),

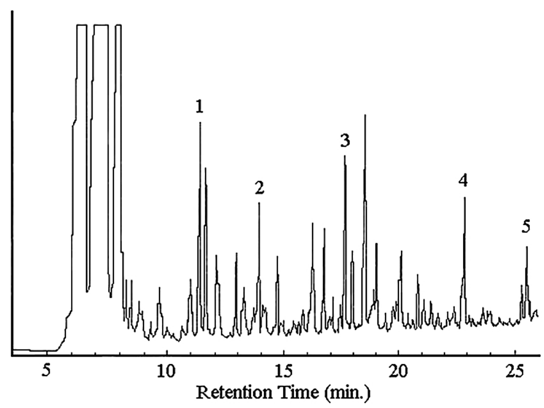

Fig. 1. Gas chromatogram of all the components from root exudates of strawberry plants adsorbed and released from activated charcoal. Methyl esters of lactic acid (peak 1), benzoic acid (peak 2), succinic acid (peak 3), adipic acid (peak 4), and *p*-hydroxybenzoic acid (peak 5) were identified based on known standard retention times (Kitazawa et al., 2005).

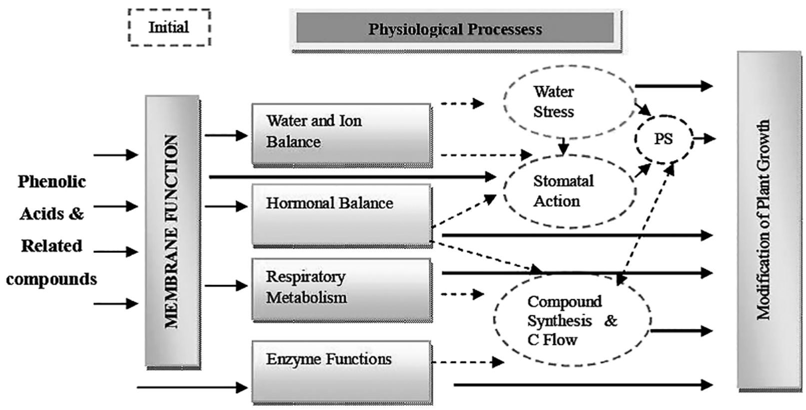

Fig. 2. A schematic diagram showing the mode of action of phenolic acid and related compounds that affects plant growth and development during allelochemical stress under recycled hydroponics. PS indicate Photosynthetic System.

photosynthesis and protein synthesis (Mersie and Singh, 1993; Rohn et al., 2002), hormonal balance (Holappa and Blum, 1991) and enzyme activities (Rohn et al., 2002; Doblinkski et al., 2003). It was reported that ion and water uptake through plant roots are the worst affected processes as they are the first organs to come into contact with autotoxins in the rhizosphere (Blum et al., 1999).

Autotoxic compounds may induce a secondary oxidative stress manifested as increased production of reactive oxygen species (Weir et al., 2004). Toxic reactive oxygen species can affect membrane permeability, cause damage to DNA and protein, induce lipid peroxidation, and ultimately lead to programmed cell death. Therefore, the autotoxic effects of strawberry plant root exudates on growth and development are likely to be caused by impairment of nutrients and water absorption due to injured roots. Supply of mineral nutrients other than by root uptake can sustain plant growth during this allelochemical stress. The availability and uptake of nitrogen is considered to be the major factor affecting growth (Lea and Azevedo, 2006); therefore, it can be sprayed on the leaves as a source of nutrients. In this case, foliar application of urea to deliver supplementary nitrogen is common (Vasilas et al., 1980; Bowman and Paul, 1992). For example, urea applied to the foliar parts of wheat had positive effects; these were attributed to higher leaf photosynthetic rates and higher leaf urease enzyme activities (Peltonen, 1993).

On the other hand, the mechanism of autotoxicity under continuous cropping showed inhibition of enzyme activity (SOD), chlorophyll content, root activity, increased MDA content, and relative permeability of cell membranes in leaves (Gao et al., 2008). The exogenous application of phenolic acids either alone or in a mixture in a simulated field experiment influenced physiological and enzymatic activities besides strawberry plant growth inhibition (Li et al., 2015). Specifically, peroxidase activity due to root exudation of strawberry under autotoxicity was found to be higher in less susceptible cultivars than mildly or highly susceptible cultivars (Weissinger et al., 2013). In another study, exogenous syringic acid was found to inhibit the net photosynthetic rate and water-use efficiency, the primary quinone electron acceptor of the PSII reaction center, the PSII reaction center and the oxygen evolving complex (Lu et al., 2018). As a result, both the maximum quantum yield of PSII primary photochemistry and the performance index on an absorption basis were depressed, resulting in reduced function of photosynthetic electron transport. The rhizosphere of strawberry replanting soil with an autotoxicity problem showed a deterioration in the physicochemical properties, enzymes activities and also the nematodes community index (Li and Liu, 2017). In recent studies, relatively high concentrations of ferulic acid in strawberry plant rhizosphere soil were thought to stimulate the growth of *Fusarium oxysporum*, thus increasing the occurrence of Fusarium wilt (Tian et al., 2019).

Autotoxicity Mitigation Methods used for Strawberry

In general, during the phenomenon of autotoxicity in vegetables and ornamental plants under closed or recycled hydroponics, released allelochemicals cause phytotoxicity. Researchers have used several methods to trap/degradate/detoxify the responsible allelochemicals of strawberry and also other vegetables. In this review, we briefly discuss the following mitigation methods: using activated charcoal, supplementation of auxin, electro-degradation of the nutrient solution, application of amino acids, application of LEDs and use of benzoic acid degrading bacteria (Table 1). Other means of improving growth inhibition due to autotoxicity such as application of GA_3, Si, and UV/H_2O_2 are also discussed briefly. In search of more suitable physical, chemical or biological methods, such research is of interest to plant biology researchers. To avoid this chemical stress in recycled hydroponics, finding a suitable allelochemical detoxifying method (mainly phenolic compounds) either in the nutrient solution or improving the impaired physiological processes would sustain crop production, including strawberry. Research findings also suggested that the growth inhibitory effect of autotoxicity on cucumber was reduced by the application of epibrassinolide, which enhanced the photosynthetic capacity of leaves, maintained chloroplast integrity and thylakoid structures, and effectively alleviated the membrane damage caused by lipid peroxidation and root damage (Yang et al., 2019).

In overcoming the continuous cropping obstacles of strawberry, a lot of research has also been conducted. Application of phenolic acid degradation fungi B3512 and medicinal plant materials have been found to have an inhibitory effect on strawberry wilt pathogen (Hu et al., 2011). Research results also showed that adding microbial soil additives could promote the growth of strawberry, improve the dry matter accumulation and yield, and reduce the degree of cell membrane peroxidation and the formation of MDA caused by continuous cropping (Gao et al., 2009). Bio-preparations of T42 *Trichoderma sp.* and Bs-6 *Bacillus subtilis* were found to significantly enhance the vegetative and reproductive growth of strawberry by inhibiting hyphal growth and spore germination of *Fusarium oxysporium* and *Rhizoctonia solani*, the main disease causes in strawberry continuous cropping (Zhang et al., 2007). The key to overcoming cropping obstacles is to improve soil permeability and reduce harmful gas contents in soil. The ecological measure applied to prevent the occurrence of strawberry replant disorder is mainly to improve the environment of the rhizosphere soil, particularly increasing the soil permeability and oxygen content (You et al., 2015). In recent studies, transcrip-

Table 1. Mitigation methods used to counter autotoxicity in strawberry plants grown in recycled hydroponics and replanting in diseased soil.

Mitigation method	Place of application	Mechanism of action	References
Activated charcoal addition	Nutrient solution	Activated charcoal adsorbs root exudate phytotoxic chemicals through its large surface area and pore spaces.	Kitazawa et al., 2005
Auxin (2,4-D and NAA) supplementation	Leaves immersed in an auxin aqueous solution	Benzoic acid disrupts the balance of endogenous hormones in strawberry and acts as an anti-auxin compound. Supplementation of NAA regulates and adjusts the endogenous hormonal balance of inhibited strawberry plants under autotoxicity.	Kitazawa et al., 2007
Biopreparation of T42 trichoderma sp. and Bs-6 Bacillus subtilis	Replanting strawberry in diseased soil	These two species inhibit the hyphal growth and spore germination of *Fusarium oxysporium* and *Rhizoctonia solani*, which are the main diseases strawberry develop in continuous cropping. As a result, the vegetative and reproductive growth of strawberry are significantly enhanced by reducing the dead seedling rate from 52.9% to 14.5%.	Zhang et al., 2007
Use of fungi B3512 and six types of medicinal plant material	Fungi applied in a culture solution and medicinal plant materials used as a substrate	Because of the fasted growth rate, the fungi B3512 inhibits the strawberry wilt pathogen while medicinal plant materials act as carbon and nitrogen sources.	Hu et al., 2011
Amino acid supplementation	Foliar application on the leaves	Autotoxic compounds impair ion uptake and hydraulic conductivity or water uptake by strawberry plant roots, leading to growth retardation. Spraying amino acids (nitrogenous compounds) can meet the nitrogen demand of strawberry plants under autotoxicity.	Mondal et al., 2013
Use of an ecological technique (soil ecological optimisation technique, SEOT)	Replanted strawberry soil was treated	SEOT is a fermented biofertilizer which consists of cow dung, straw, and antagonistic actinomycetes that can prevent the occurrence of strawberry replant disorder mainly due an improvement in the environment of the rhizosphere soil, particularly by increasing the soil permeability and oxygen content.	You et al., 2015
Electro-degradation	Nutrient solution	Phenolic chemicals (mainly benzoic acid) present in recycled hydroponic culture solution are oxidized rapidly at the anode of the electrode and decompose to CO_2 after electro-degradation treatment.	Asao et al., 2008 Asaduzzaman et al., 2012 Talukder et al., 2019
LEDs and amino acids supplementation	Plants grown under LEDs and foliar application of amino acids on leaves	Light conditions affect the rate of release of root exudates, including benzoic acid, which is a secondary metabolite linked with photosynthesis. Higher intensity red light is the most effective to enhance photosynthesis in strawberry plants under recycled hydroponics.	Talukder et al., 2018
Use of benzoic acid-degrading bacteria	Enrichment and isolation of degrading bacterial strains	The inoculated bacterial strains use benzoic acid as their sole carbon source and the amount of residual benzoic acid was found to decrease with gradual increases in degrading bacteria.	Ziying et al., 2018

tomic profiling of strawberry roots in soil with and without soil amendment revealed gene expression changes in genotype-dependent responses (Chen et al., 2020). There was an overall increase in the expression of nutrient transport genes and a decrease in the expression of defense response genes, which could be one mechanism underlying a recovery strategy in strawberry roots.

Adsorption of allelochemicals in activated charcoal

The removal of inhibitory allelochemicals from the culture solution can allow continued crop cultivation for several cultures. Therefore, elimination of these growth inhibitors from the recycling culture solution is desirable for conservation-oriented agriculture. In hydroponic culture systems, allelochemicals released through plant roots can easily be trapped and isolated using activated charcoal as applied in the recycled hydroponics of strawberry (Fig. 3; Kitazawa et al., 2005). A number of researchers suggested addition of activated charcoal to the culture solution to improve the growth and yield by adsorbing organic compounds (mainly phenolics) in tomato (Yu and Matsui, 1993), strawberry (Kitazawa et al., 2005), taro (Asao et al., 2003), cucumber (Yu and Matsui, 1994; Asao et al., 1998, 1999b, 2000), several leafy vegetables (Asao et al., 2004a), and some ornamentals (Asao et al., 2007).

Activated charcoal has a strong capacity for adsorbing organic chemicals and is an ideal adsorbent for practical agricultural use. It has also been found to adsorb allelopathic plant exudates in soil with few effects on soil nutrients (Callaway and Aschehoug, 2000). Because of its very large surface-to-volume ratio, activated charcoal can adsorb organic compounds in soils (Zackrisson et al., 1996), and has been used both in greenhouse and field experiments (Zackrisson and Nilsson, 1992; DeLuca et al., 2002; Prati and Bossdorf, 2004; Thoss et al., 2004; Callaway et al., 2005; Kulmatiski and Beard, 2006). Earlier research results reported that under in vitro conditions, addition of activated charcoal to a medium for plant tissue cultures could improve growth by adsorbing toxic metabolites (Wang and Huang, 1976).

A number of studies have used activated carbon to neutralize the effects of allelochemicals (Mahall and Callaway, 1992; Nilsson, 1994; Callaway and Ashehoug, 2000; Inderjit and Callaway, 2003; Kulmatiski and Beard, 2006). Activated charcoal with its large surface area and pore volume, as well as its polarity, has tremendous adsorptive capacity and complex chemical and physical properties. Its activity can be separated into adsorption, mechanical filtration, ion exchange, and surface oxidation (Cheremisinoff and Morresi, 1978). Therefore, application of activated charcoal can be a good tool for studies of allelopathy because it acts as an adsorbent for many large organic compounds (Cheremisinoff and Morresi, 1978).

The use of activated charcoal is an interesting experimental tool, but its high cost precludes its commercial application. Moreover, it was found to adsorb Fe-EDTA in a nutrient solution and subsequently created an Fe deficiency in plants (Yu et al., 1993). Although it has been shown to be highly effective in the laboratory setting, field performance studies are needed to investigate its long term effects on the alleviation of autotoxic compounds and on soil physical and chemical properties in the subsequent culture. Activated biochar charcoal had a positive influence on seed germination and early seedling development of maize and radish seeds through the adsorption of allelochemicals, as well as on strawberry guava (*Psidium cattleianum*) and lemongrass (*Cymbopogon flexuosa*) under tropical island invasion (Sujeeun and Thomas, 2017). In another study, the adsorption performance on granular activated carbon, ion exchange and ozonation was evaluated; benzoic acid produced at 23 $\mu g \cdot L^{-1}$ in a reused nutrient solution was completely removed by granular activated carbon adsorption, ion exchange or an ozonation process (Hosseinzadeh et al., 2017).

Growth improvement by supplementation of auxin, GA_3 and Si to the nutrient solution

The nutrient solution contains many potential substances that can inhibit the growth and yield of strawberry. In recycled hydroponics, absorption of water and mineral nutrients is impaired by chemical interference in the culture solution. Under such conditions, supple-

Fig. 3. Hydroponic system used for strawberry cultivation (left). Air filter filled with 100 g of activated charcoal attached to an air pump in a solution container (right). The activated charcoal was replaced at two-week intervals until harvesting. The used activated charcoal was either immediately extracted with organic solvents or stored at 5°C for later extraction (Kitazawa et al., 2005).

mentation of 5.4 μM NAA appeared to be the most effective concentration in ameliorating the inhibited vegetative growth of strawberry plants (Kitazawa et al., 2007). It was found that the number of flowers and harvested fruit of strawberry increased with auxin treatment, but was reduced by autotoxicity. In earlier studies, Kitazawa et al. (2005) reported that benzoic acid was the strongest inhibitor of vegetative and reproductive growth in strawberry. It was also suggested that phenolic compounds disrupt the balance of endogenous hormones in plants (Rice, 1984). Thus, benzoic acid exudated from the roots may be absorbed and disrupt the balance of endogenous auxin in strawberry.

Phenolic compounds, including benzoic acid, disrupt the balance of endogenous hormones in plants (Rice, 1984; Asao et al., 2001). Some substituted benzoic acids or compounds having a benzoic acid-like structure such as trans-cinnamic acid (Van et al., 1951), chlorobenzoic acids (Keitt and Baker, 1966), and 2,3,5-triiodobenzoic acid (Karabaghli-Degron et al., 1998), are considered anti-auxin. It was also reported that auxin controls several fundamental functions including hormonal regulation of plant development (Lomax et al., 1995; Hobbie, 1998; Berleth and Sachs, 2001). In strawberry, fruit expansion and maturation reportedly depends on auxin (Callis, 2005). Thus, benzoic acid exudated from strawberry roots may reduce the auxin activity and inhibit fruit enlargement. It is known that auxin controls several fundamental functions in plant development processes such as cell expansion and division, lateral root formation, vascular differentiation, and shoot elongation (Lomax et al., 1995; Hobbie, 1998; Berleth and Sachs, 2001). In deep water culture, various morphological and physiological traits such as biomass accumulation, leaf expansion, stomatal conductance, water use efficiency, and the nitrogen use efficiency of leaf lettuce and rocket, were found to be enhanced by 10^{-6} M GA_3 addition to the nutrient solution (Miceli et al., 2019). In another study, it was reported that Si significantly enhanced the α-amylase activity and gene expression in melon seeds under autotoxicity, and promoted the degradation of starch. The effect of Si on antioxidant enzymes and MDA content in seeds at the early stage of germination under autotoxicity was not obvious. In the late stage, the addition of Si significantly alleviated the inhibition of antioxidant enzyme activity by autotoxicity, and maintained the MDA content at a relatively normal level. Si treatment is an effective strategy to improve the resistance of melon seeds to autotoxicity (Zhanga et al., 2020).

Addition of electro-degradation and UV/H_2O_2 to the nutrient solution to degrade root exudates

Allelochemicals present in root exudates are accumulated in the recycled culture solution. Mitigation through degradation of root exudates could have a preventive role in growth retardation during this chemical interference. A great number of studies reported that detoxification of allelochemicals including phenols (Fleszar and Ploszynka, 1985; Comninellis and Pulgarin, 1991; Feng and Li, 2003), catecol (Comninellis and Pulgarin, 1991), and hydroquinone (Fleszar and Ploszynka, 1985; Comninellis and Pulgarin, 1991), as well as benzene can be decomposed through electro-degradation (Fleszar and Ploszynka, 1985). These studies indicated that phenolic chemicals present in the treated solution are oxidized rapidly at the anode electrode and decompose to CO_2.

In later studies, electro-degradation was applied to decompose benzoic acid exuded into the nutrient solution from strawberry plants. It was found that fruit yield increased significantly after applying electro-degradation to a strawberry recycled nutrient solution for 24 h at 2-week intervals (Asao et al., 2008). This study suggested that frequent electro-degradation (less than 2-week intervals) may be more effective to alleviate autotoxicity in strawberry. At the same time, it has been found that the concentration of Fe-EDTA in an electro-degraded solution decreased following electro-degradation treatment. The Fe-EDTA concentration decreased by about 90% from the initial level after electro-degradation while this value was found decrease 30% without electro-degradation solution after 24 h. It has been reported that at a normal concentration, Fe-EDTA decreases due to ultraviolet degradation (Date et al., 2002) and/or microbial decomposition, including

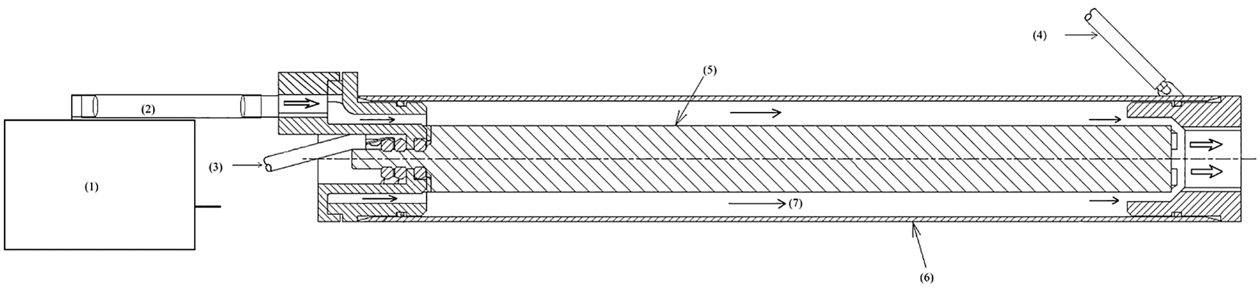

Fig. 4. Schematic diagram of the electrode used for the electro-degradation treatment. Different components are as follows: (1) pump, (2) plastic tube connecting pump with electrode, (3) anode, (4) cathode, (5) central ferrite core, (6) cylindrical titanium pipe, and (7) nutrient solution flow (Asaduzzaman et al., 2012).

anodic degradation (Kusakabe et al., 1986). Asao et al. (2008) recommended adjusting the Fe-EDTA concentration after electro-degradation and conducting further experiments to determine the appropriate timing and intensity of electro-degradation.

In follow up studies, the appropriate timing and intensity of electro-degradation was investigated and it was found that electro-degradation for 2 h every four weeks recovered autotoxicity in strawberry in Wagner's pot hydroponic system (Asaduzzaman et al., 2012). For electro-degradation, an electrode having a central ferrite core enclosed with a titanium tube coupled with a DC power supply is used (Fig. 4; Asaduzzaman et al., 2012). The electricity for electro-degradation is maintained at 2 amps for 2 h. In a without plant experiment, it was noted that 24 h electro-degradation of the nutrient solution was associated with a decline in the Fe-EDTA concentration (about 10%), a lower concentration of Ca^{2+} (about 66% of the initial level), low pH (3.1) and an increase in temperature (9.1°C) in the treated culture solution; these problems did not appear with a 2 h application (Asaduzzaman et al., 2012).

Recently, it has been reported the above problems associated with direct current electro-degradation can be solved using alternate current electro-degradation (Fig. 5; Talukder et al., 2019). It is hypothesized that with alternate current electro-degradation both positive and negative charges of the electrodes (anode and cathode) change frequently and thus iron and calcium ions may not be precipitated to the electrode. This study also suggested that alternate current electro-degradation of the nutrient solution (300 L) for 24 h once every three weeks could be applied for greater recovery of strawberry yield (about 86%) grown in a closed hydroponic culture system as shown in Fig. 6. In a recent study, it was found that the degradation of benzoic, phthalic and succinic acids present in a reused nutrient solution could be achieved through UV/H_2O_2 application and the amount of benzoic acid removed increased from 83% to 91% when increasing the contact time from 90 min to 270 min in the presence of 50 $mg \cdot L^{-1}$ H_2O_2 and with UV application (Hosseinzadeh et al., 2019).

Growth improvement of strawberry through foliar application of amino acids

Allelopathic compounds have been reported to enhance secondary oxidative stress leading to production of reactive oxygen species (Weir et al., 2004). These species can affect membrane permeability, cause damage to DNA and protein, induce lipid peroxidation, and thereafter ultimately lead to programmed cell death of roots. Growth of strawberry plants is retarded due to impairment of nutrient and water absorption by injured roots under autotoxicity. Supply of mineral nutrients other than by root uptake can sustain plant growth under such allelochemical stress. Amino acids are nitrogenous compounds that can be absorbed by leaves exogenously (Furuya and Umemiya, 2002). It has been reported that improvements in growth, yield and quality of different crops such as garden croton (Mazher et al., 2011) and Japanese pear (Takeuchi et al., 2008) can be achieved through foliar application of amino acids. Amino acids protect plants in several ways through cellular osmotic adjustments, detoxifying reactive oxygen species, maintaining membrane integrity, and stabilizing enzymes or proteins (Yancey et al., 1982; Bohnert and Jensen, 1996). Proline has been reported to accumulate under drought conditions (Choudhary et al., 2005), high salinity (Yoshiba et al., 1995), high light

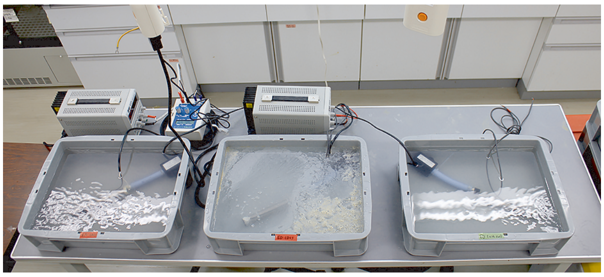

Fig. 5. Electro-degradation of nutrient solution after a without plant experiment for 24 hours. Alternating current—electro-degradation (AC-ED) was applied at a 50% duty ratio, 2.0 amperes alternate current, and 14.0 volts (left). Direct current—electro degradation (DC-ED) was applied at 2.0 amperes and 18.0 volts (middle). Control-without ED application; the nutrient solution was flowed using the pump only (right) (Talukder et al., 2019).

Fig. 6. Three-layered vertical growing beds used for cultivation of strawberry plants under controlled-environment agriculture. Each grow bed had 50 L nutrient solution capacity and three beds placed vertically were connected to a tank filled with 300 L nutrient solution (left). Strawberry plants grown in recycled hydroponics with alternate current electro-degradation (right) (Talukder et al., 2019).

and UV irradiation (Saito et al., 2012), heavy metal exposure (Saradhi et al., 1995), and in response to biotic stresses (Fabro et al., 2004; Haudecoeur et al., 2009). As plant growth recovers from the detrimental effects of stresses via the over-production of amino acids, many researchers have suggested that the application of exogenous amino acids may improve the growth and yields of stressed crops (Schat et al., 1997; Maini and Bertucci, 1999; Heuer, 2003). Recent studies have revealed that exogenous amino acids can be absorbed by leaves (Furuya and Umemiya, 2002; Stiegler et al., 2013).

In recycled hydroponics, continuous accumulation of allelochemicals creates stress conditions for strawberry plants that can be improved by amino acid spraying. In this regard, of 22 amino acids sprayed on strawberry plants grown using recycled hydroponics, glutamine and hydroxyproline were found to improve fruit yield by over 50% (Mondal et al., 2013). It has been reported that the total dry mass of strawberry plantlets was greatly improved by the application of urea, hydroxyproline, glutamine, and GABA under *in vitro* conditions. Recent studies also found a positive influence of amino acids under an *in vitro* condition as an organic source of nitrogen in alfalfa, maize, sorghum, pineapple, rice and sugarcane (Skokut et al., 1985; Claparols et al., 1993; Rao et al., 1995; Hamasaki et al., 2005; Grewel et al., 2006; Asad et al., 2009).

Application of LEDs to recycled hydroponics in plant factory strawberry production

Application of LEDs with a precisely adjusted light spectral composition may provide improved control over plant stress responses. Recently, LED supplemental lighting was reported to accelerate photosynthetic activities and promote the growth of strawberry plants (Hidaka et al., 2013). A comparison of the photosynthetic rates of strawberry leaves exposed to red (660 nm) or blue (450 nm) LEDs indicated that red light led to higher quantum efficiency (Yanagi et al., 1996), while blue LEDs at 30 $\mu mol \cdot m^{-2} \cdot s^{-1}$ or red LEDs at 100 $\mu mol \cdot m^{-2} \cdot s^{-1}$ were found to restore chlorophyll synthesis in wheat seedlings (Tripathy and Brown, 1995). Other researchers also observed better plant responses to red and blue LED combinations in various crops, including increased total biomass in red leaf lettuce (Stutte et al., 2009), enhanced chlorophyll a and b accumulation in kale (Lefsrud et al., 2008), and increased growth of lettuce, spinach, and radish (Yorio et al., 1998).

It has been reported that long-wavelength red light could enhance phenolic compound accumulation, while short-wavelength blue light could enhance the biosynthesis of flavonoids and lactones (Xie, 2002). The amount of rosmarinic acid, a major component of phenolic compounds in sweet basil was found to vary under continuous red and white light or blue light (Shiga et al., 2009; Shoji et al., 2009). Supplemental UV-B light at 2.5 $\mu mol \cdot m^{-2} \cdot s^{-1}$ for 1 h each day and 2 h each day for a week significantly increased the content of total phenolic compounds and anthocyanin concentrations in sweet basil, with the short UV-B treatment being more efficient for anthocyanin accumulation than the long UV-B treatment (Sakalauskaite et al., 2012). Therefore, light conditions may also influence the rate and amount of growth inhibitors released, including benzoic acid, which is a secondary metabolite associated with photosynthesis. Light-emitting diodes have recently attracted attention as an artificial light source for plant production because of their long life and lower heat emission and power consumption compared to fluorescent lamps. They are capable of emitting a narrow wavelength band, and can produce high-quality light suitable for plant growth. Exposure to a combination of red light (600–700 nm) and blue light (400–500 nm) induces diverse effects on plant growth and development. Additionally, photosynthetic activities were found to be particularly effective under red and blue light (Sadak et al., 2015). Therefore, improving retarded growth and yield of strawberry under autotoxicity through application of different quality and intensity of growth lights, along with amino acid supplementation, would be highly beneficial for sustainable crop production.

It was found that plants exposed to a high-light intensity R:B = 8:2 LED showed greater growth; however, a direct relationship between the LED lighting and magnitude of allelochemical exudation has not been reported (Talukder et al., 2018). It was hypothesized that higher intensity red light LED would enhance photosynthesis in strawberry plants. In earlier research, it was reported that red wavelengths (600–700 nm) were efficiently absorbed by plant pigments (Sager and McFarlane, 1997) and LEDs emitting at 660 nm were considered to be most efficient; this is close to the absorption peak of chlorophyll that saturated phytochrome, resulting in a high-Pfr photostationary state (Massa et al., 2008).

Summary and Further Research Thrust

A better understanding of the molecular processes involved in autotoxicity and the actual secretion of phytochemicals by roots. Greater understanding of root exudation from the molecular to the ecosystem scale will potentially lead to the development of better plants capable of absorbing more nutrients, detoxifying soils more efficiently, and more effectively warding off invasive weeds and pathogenic microbes. A detailed analysis of the genotypic differences in autotoxin metabolism, exudation and associated changes in knockouts plants and plant growth will generate important evidence for autotoxicity in these crops. In addition, there is a need to understand the underlying mechanism and regulation of root exudation that supports utilization of phytochemical production for enhanced agricultural benefit. A major challenge for researchers is to characterize new transport systems and regulatory mechanisms involved in the root secretion process. In this regard, a greater understanding of root-secreted phytochemicals and their role in the rhizosphere will be useful in determining the link between below-ground and aboveground interactions and vice versa, and also the abiotic factors that interact with biotic factors to drive ecosystem properties.

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